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STATUS OF ENDOCEROID CLASSIFICATION

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ABSTRACT—Problems in endoceroid classification stem largely from the fragmentary nature of most specimens. Indeed, this is the main contributing cause to the fact that one group of genera is based upon adult features, another on early stages, and a third group on features of the endosiphuncle. Appalling problems in nomenclature and priority result. The morphology of the endoceroids is summarized, pointing out the wide variation in structure of siphuncle wall and features of the endosiphuncle. Growth relationships of the parts are discussed. The endosiphuncle. is regarded as representing calcification within the tissues of the siphon; the tubes functioned to supply abundant blood necessary where active lime secretion occurred; the blades are reflections of supporting tissues, and not analogous to the radial canals of actinoceroids.

The general evolutionary pattern within the endoceroids is outlined, and the relationship of some anomalous genera is discussed. Brief mention is made of the known features and those features not known from present material which require study. The features of *Endoceras*, *Vaginoceras* and *Cameroceras* are summarized, and the scope of the genera is discussed.

Three new genera exhibiting remarkable features, are described in detail. *Hudsonoceras* is regarded as stemming from the Proterocameroceratidae through *Coreanoceras;* and *Allotrioceras* and *Mirabiloceras*, constituting the new family Allotrioceratidae, seem traceable also to the Proterocameroceratidae independent of the Endoceratidae, through *Meniscoceras.*

INTRODUCTION

THIS is an attempt to reduce the confusion which surrounds some of the largest fossils known in the Ordovician, the endoceroids. They are not all large, by any means, but specimens twelve feet in length have been collected, and fragments of greater diameter indicate a much greater maximum length. I am not wholly inclined to discredit a report of an endoceroid found in a quarry near Watertown New York, which was measured before it was broken up and found to attain a length of 30 feet.

With the exception of the piloceroids, which sometimes attained striking forms, most of the endoceroids are straight slender shells, rather nondescript externally. A collection of them seems about as fascinating as a collection of telegraph poles. The removal of even reasonably complete specimens involves something very close to quarrying operations; storing them is another problem. They require too much space. For this reason, our collections contain scarcely any endoceroids which are even reasonably nearly complete.

More often the large shells were badly broken before burial. The problem is then posed of determining the specific identity of different parts, which is still further

complicated by the varying aspects of different growth stages and vicissitudes of preservation. Pieces with living chambers and septa rarely extend far enough to preserve the endocones. The parts of the siphuncle which were filled with cones are often broken off, abraded, and often deposited together, apart from the later shell stages. The extreme apices are rare, and usually separated even from the larger, solid, later parts of the siphuncle.

The puzzle presented by these fragments has resulted in as bad a taxonomic system as that which a generation ago obscured the study of fossil trees, which had the roots in one genus, the trunk in a second, stems in a third, leaves in a fourth, and fruiting bodies in a fifth. Some endoceroid genera are based only upon the features of the late stages. Practically no attention has been paid to the structure of the siphuncle wall; it was thought to be uniform throughout the group. Other genera have been established primarily upon the features of the endosiphuncles. Still another group of genera have been based upon the early stages; such are *Nanno*, *Suecoceras*, *Cameroceras* and *Foerstellites*.

For the past fifteen years the writer has been interested in attempting to solve the taxonomic problems thus presented. As yet, the results are only partially successful. However, in the process, it has become evident that the endoceroids are a group structurally diverse beyond the wildest imaginings of those who have never examined them beyond the scope of the ordinary textbook. Further, the structures supply a basis for a refined taxonomy, as a result of which the species are resolved into genera of appreciable faunal and stratigraphic significance.

The present work is confined to a summary of the problem encountered, a survey of the morphology, a summary of investigations of a few of the older and long used—or misused—generic names, and the description of some new types exhibiting some amazing structures. Another paper, now in an advanced stage of preparation, will deal with the descriptions of some isolated silicified siphuncles from the Canadian. There, silicified endoceroids are sometimes prominent among the very few fossils preserved in the dolomites. The indications of this study are that there are many characteristic endoceroids which can be recognized from the siphuncles alone. On this basis an amazing correlation has been found possible among the endoceroids of the horizons of the Canadian of New Mexico, Maryland, and New York which far exceeded any original expectations.

The investigation of the endoceroids is, however, even yet in a stage somewhat comparable to that of the Bryozoa when the first few thin sections had been made. Indeed, the present work is published primarily in the hope of calling wider attention to the variations in structure, and the rich reward in faunal and stratigraphic information which promise to reward the study of these long neglected fossils.

MORPHOLOGY

Shell wall.—As in most cephalopods, the shell walls are usually so replaced that their original fine structure cannot be determined. There remain two features to be noted: form and ornament. Most endoceroids are straight slender shells, except for the apices which are blunt and rapidly expanding. Some are gently curved endogastrically, never exogastrically. *Cyrtendoceras* is a relatively slender endogastric gyrocone. In the Canadian there developed rapidly expanding shells with extremely rapidly expanding, broadly conical siphuncles, the piloceroids. Such shells are straight or gently endogastric cyrtocones. A form soon to be described from the El Paso limestone, proved to be as strongly curved as *Cyrtendoceras*, though completely unrelated to that genus. Some of the piloceroids become slender in late growth stages; in some the aperture of the shell even contracts. There results among these rarer forms an almost bewildering variety of shell shapes.

Most endoceroid shells are smooth. A few genera are annulated, but are not for this reason closely related. *Cylendoceras*, Grabau and Shimer, (1910) is an annulated member of the Endoceratidae. *Anthoceras* Teichert and Glenister and *Campendoceras* Teichert and Glenister (1954) both appear to be members of the Proterocameroceratidae. The position and validity of *Kawasakiceras*

Kobayashi (1934) remain to be determined.

It is worthy of note that the conchial furrow (Flower, 1939) present in most nautiloids, has not been noted in the Endoceratida, Ellesmeroceratida or Actinoceratida.

Septa.—The septa are relatively simple except for the developments of the septal necks. The septum is divided into a mural part, a free part and a septal neck. The sutures may develop lateral lobes, or either dorsal or ventral lobes or both, but are never complex. The septal furrow common to most nautiloids, has not yet been observed in the endoceroids.

Siphuncle wall.—The siphuncle wall consists of septal necks and connecting rings. Some of the variations in structure have already been shown (Flower, 1941, 1947), and others are shown in Text-figure 1.

The oldest of the endoceroids have essentially the pattern of the older Ellesmeroceratidae, including a strong similarity in the siphuncle wall. The septal necks are extremely short, and supplemented by thick rings, homogeneous in structure, or differentiated into layers. This pattern is in general characteristic of the slender Canadian endoceroids, which are grouped on that basis in the family Proterocameroceratidae.

Within this group, however, there is a gradual prolongation of the septal necks. As the necks grow the connecting ring continues to stretch from the tip of one neck apicad to the tip of the next preceding septal

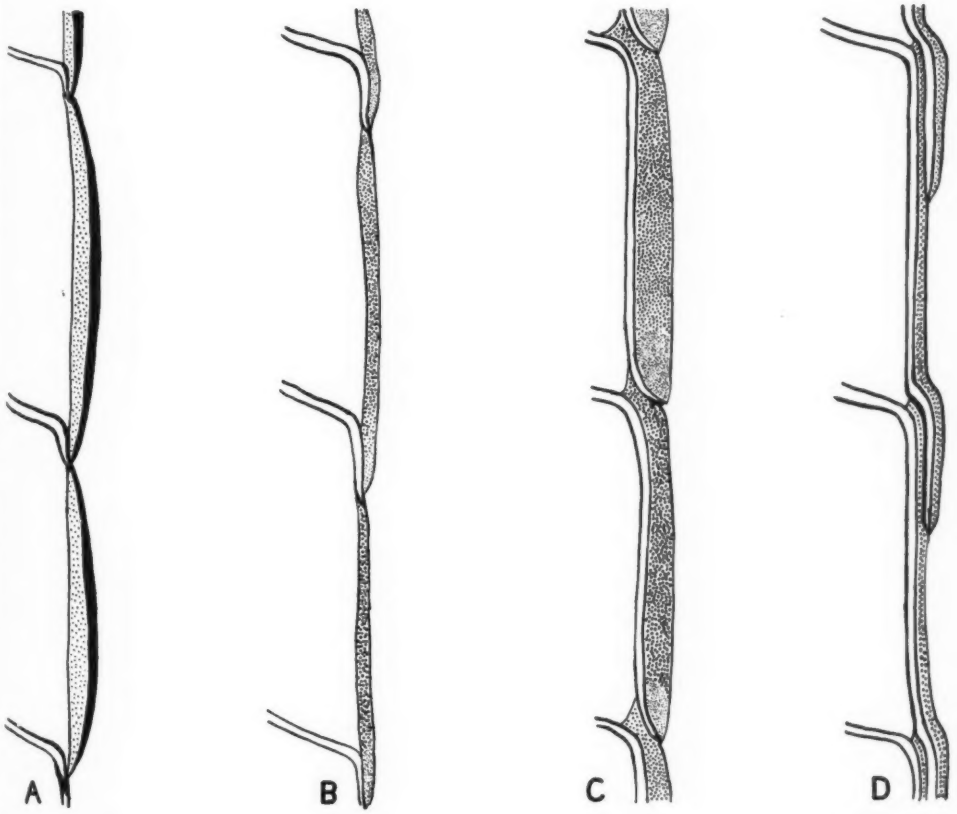


FIG. 1—Progressive prolongation of septal necks in the Endoceratida. A. Necks aneuchoanitic, connecting ring layered. B. Septal necks lengthened slightly, ring showing no clear differentiation of structure. C. Necks elongated to a holochoanitic condition; tip of ring differentiated into eyelet. D. Necks prolonged into second segment, with ring beginning in interval of overlapping parts. Eyelet not well differentiated.

neck. As this occurs, the tip of the ring which lies within the preceding neck tends to develop into a region of dense amorphous material, the eyelet. (Text-fig. 1, B, C.) When, however, the necks pass the holochoanitic condition, so that the tip of one neck is invaginated into the next, a modification occurs. Then the connecting ring begins at a point where the two septa are nearly in contact, instead of at the tip of the neck, and extends between the necks which are now narrowly separated. Beyond the tip of the inner neck, the ring extends along the inner surface of the outer neck to its very tip. Sections of some Canadian genera, notably *Clitendoceras*, indicate that there is an as yet unsuspected complication in the siphuncle wall of some endoceroids: the neck may be very short in young stages and increase in length rapidly in succeeding camerae so that it is nearly holochoanitic in the adult stages. The necks are, however, uniformly holochoanitic throughout the ontogenetic stages of the known Endoceratidae.

Isolated siphuncles often show annular septal markings. Where the siphuncle is marginal, as is usually the case, the septa slope strongly apicad from the venter to the dorsum. The annulations thus supply valuable criteria of orientation. Occasionally, siphuncles exhibit a broad annular pattern independent of and on a broader scale than the spacing of the septa, as noted in *Kotoceras cylindricum* Kobayashi (1934, pl. 12, fig. 8). In general, the appearance of septal annulations must be used with great caution in taxonomy. Siphuncles which may be markedly annular in young stages may become nearly cylindrical in mature parts of the shell. Isolated siphuncles are often exfoliated endosiphuncles, with septal necks and connecting rings lost. If the connecting ring is thick, the surfaces of such specimens may be relatively smooth, even if the septal neck is definitely concave between the septa. The connecting ring, by variations in thickness, tends to smooth out the outline. This is particularly true of typical *Vaginoceras*. Furthermore, the presence or absence of annular markings can be greatly modified by abrasion of isolated siphuncles prior to burial.

Endosiphuncle.—The solid filling of calcareous material within the siphuncle wall was termed the endosiphuncle by Ruedemann (1905). In most cephalopods its differentiation is largely academic; but in the endoceroids, in connection with which the term was first proposed, it is an entity in itself. The growth relationships of the endosiphuncle with the shell as a whole have been misunderstood. Sardesson (1930) remarked that some endoceroids had them better developed than others; still others seem to lack them. This is not strictly true. Some specimens seem to lack them, some show them better developed than do others, but it must be remembered that such specimens are incomplete. Fischer (in Moore, Lalicker and Fischer, 1952, p. 344) has presented a diagram showing the function of endocones in maintaining the balance of the endoceroid shell. There is always an adoral interval of phragmocone enclosing a length of siphuncle free from endocones. The apical concentration counteracts the buoyant effect of the gas-filled camerae, making it possible for the animal to live with the shell in a horizontal rather than a vertical position. Close adjustment with growth of the shell as a whole indicates that probably the endocones were so developed as to maintain a center of gravity close to the midlength of the shell throughout life. The large ventral siphuncles doubtless served also as a stabilizing device. Further, the heavy apical ends of such forms as *Nanno*, may have aided hyponomic swimming.

It should be noted that in large endoceroids a very large interval of the adoral part of the phragmocone may lack the endocones. Fragmentary specimens of phragmocones may lack cones, show the last endocone, or contain a part of the siphuncle which is filled solid with calcareous material, depending upon their original distance from the living chamber. Such specimens are the basis of the concept that the growth of the endocones is variable in some endoceroids. While understandable, this conclusion is regarded as unsound. A specimen of *Endoceras* from the Trenton limestone showed 28 inches of phragmocone and the base of a living chamber. Only at the extreme apical end of this specimen did the last endocone appear. In *Hudsonoceras aristos* the adoral 22 inches of the phragmocone shows no trace

of endocones. In general, the length of the siphuncle which is free from endocones is roughly proportional to the diameter of the shell at the base of the living chamber.

The growth relationships of such a form as *"Vaginoceras" appletum* Ruedemann are shown in Text-figs. 2A–H. The initial shell must have lacked septa, as in Text-fig. 2A. Text-fig. 2B shows the first septum, 2C a slightly later stage. Not until septation is well advanced (Text-fig. 2D) does the first trace of the endocones of the endosiphuncle appear. The siphuncle which is first rapidly contracted, lies so close to the venter that it is sometime almost impossible to make out its wall structure there. As shown in Text-figs. 2F–H (cross sections taken at c, b and a, respectively, in Text-fig. 2D) the siphuncle

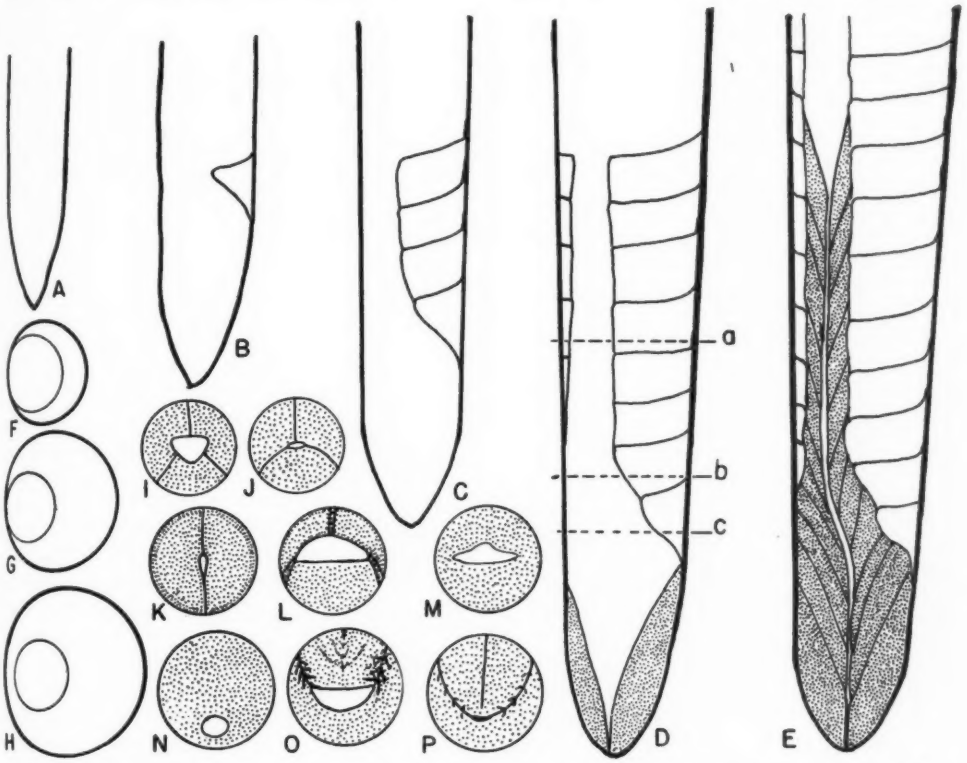


FIG. 2—General morphological features of the Endoceratida. Figures A–E are vertical longitudinal sections of growth stages of an advanced endoceroid, based largely upon *"Vaginoceras" appletum* Ruedemann. A. Early stage without septa. B. The first septum is secreted after further growth of the shell. C. Additional septa are formed, but endocones are still wanting. D. After the development of appreciable interval of the phragmocone the first endocones are secreted. E. Endocones have advanced, filling an appreciable part of the siphuncle. The complete shell would be about twice the length of the portion shown in this figure. F. Cross section at c on figure D. G. Cross section at b of figure D. H. Cross section at a of figure D. These three figures show the relative decrease in size of the siphuncle and its removal form the ventral wall of the shell.

I–P. Cross sections through endosiphuncles showing variations in the shape of the cones, position of tubes, and number and arrangement of the blades. I. Triangular cone with three blades, found in some Trenton species currently assigned to *Endoceras*. J. Depressed elliptical tube supported by three blades, found in Cincinnatian species currently included in *Endoceras*. K. Vertical blades supporting a compressed cuneate cone or tube, characteristic of *Vaginoceras*, sensu stricto. L. Semicircular cone and complex blades of *Coreanoceras*. M. Broadly triangular cones characteristic of some Eden species currently included in *Endoceras*. N. Circular cone terminating at a point close to the ventral wall of the siphuncle, found in what is regarded as typical *Endoceras proteiforme*. O, P. Sections through cone and tube respectively of *Meniscoceras coronense*, showing reversed orientation of semicircular cone and blades from *Coreanoceras*.

becomes proportionately smaller in relation to the shell, and eventually more removed from the ventral wall, though this feature varies from one species to another. Where the growth of the shell continues further, the endocones advance in growth, at length filling an appreciable length of the siphuncle. It should be noted however, that with such development as shown in Text-fig. 2E, there would be a missing portion about equal to the length represented lying between the last bit of endocone material and the base of the living chamber. With further growth, this length would remain about the same, while the length of the endocone would increase.

Lining.—Ruedemann (1905) attributed to many endoceroids an organic lining in the siphuncle which developed prior to the deposition of the endocones. I have found such structures to be the exception rather than the rule. Inorganic calcite may sometimes present the appearance of such a lining. Cross sections through siphuncles indicate such a lining but are probably only a reflection of tissue differentiation. Such markings are similar in color and composition to the blades which join them, and are discussed more fully below. The only good lining I have observed is in the genus *Allotrioceras*, described below.

Endocones.—The solid filling of the siphuncle is commonly in the form of cones. Their apices point toward the tip of the shell, and are commonly joined by a continuous tube. Usually the cones are seen as regions of light calcite separated by thin dark bands. The dark bands represent resting stages in the growth of the endosiphuncle, and the consequent incorporation of excess organic material at these regions. The spacing and clarity of the margins of cones is highly variable. Recrystallization can remove all traces of these structures, and doubtless accounts in part for the obscurity of the bands in apical parts of siphuncles. I am inclined to believe, however, that there is another cause. As cones are traced apically, their margins often become gradually fainter, in a gradual way which is not always consistent with the degree of obvious recrystallization. It may well be that the growth of cones was more rapid in the initial part, and that the clarity of their boundaries varies to some extent with the time lapses in their deposition. Inasmuch as some readjustment of balance was necessary in the animal when the first cones were built, the hazards accompanying this change would be reduced if the transition period was shortened. It is therefore reasonable to believe that the apical absence of cones in some forms may be a reflection of rapid growth of the initial part of the endosiphuncle. Indeed, in *Allotrioceras*, described below, the cones are absent apically although other fine structures, notably the radial tubes, are preserved in the greatest detail. Recrystallization is not a convincing explanation for the phenomena observed; rather, deposition seems to have continued uninterrupted over a considerable interval of the early part of this siphuncle.

The endocones vary widely in shape and form. They may be smooth, annulated, and occasionally fluted. One thinks of these cones as circular in cross section, and this is often true. Text-figs. 2I–P show some of the variations in cross section what have been observed in the endoceroids.

The surface of the last endocone is commonly preserved as the speiss, or tip of the mud filling of the siphuncle. Its cross section and surface features are often highly characteristic. Except where siphuncles are silicified and can be dissolved from the matrix, it affords the only opportunity for a detailed study of the endocone surface, which may contain faint markings often not apparent from sections.

The surface of the endocone may vary in ontogeny. A piloceroid, soon to be described, has a simple cone terminating in a centrally located tube throughout most of its life. In late stages, however, the tip of the cone moves close to one side and the cone is correspondingly distorted.

Tube.—The tube (endosiphotube of Ruedemann, 1905) extends from the tip of the last endocone toward the apex of the shell. It was at one time believed to terminate in an apical cicatrix, and thus to serve as a potential channel to the exterior. It is possible that this is true, but actual determination of the tube to the very apex, and the presence there of a perforation through the connecting ring forming the apical caecum, and through the shell wall, require further confirmation.

The tube may be circular in cross section,

flat or curved, depressed or compressed. In longitudinal section tubes are sometimes faintly annular. Again, they may be crossed by diaphragms reminiscent of those crossing the whole siphuncle of the Ellesmeroceratidae. They may vary in form with ontogeny. Ruedemann (1905) regarded the round tube of the apical end of *Proterocameroceras* as giving way adorally to a flat tube which he called the endosiphocoleon. In other endoceroids this sort of differentiation has not been found. Having observed the structures in detail, I am uncertain whether the cones of *Proterocameroceras* terminate in a flat coleon which is then filled in laterally leaving only a small round tube, as Ruedemann suggested, or whether an initially circular small tube gives way in late ontogenetic stages to the flat tube known as the endosiphocoleon. Ruedemann's sections, as well as many supplementary sections which I have made, could be interpreted either way.

The most amazing development of the tube is the multiple series of tubes found in the early stages of *Allotrioceras*, and in the adult of *Mirabiloceras*. Both are described below, and nothing like them has been reported previously.

Blades.—Cross sections of the endosiphuncle apicad of the speiss often show a series of dark lines running from the tube toward the periphery of the siphuncle. Often they join there a dark band running just within the periphery of the endosiphuncle. These radial bands were named endosiphoblades and have been noted by Dewitz (1880), Schröder (1881), Holm (1885), Foord (1888) and Ruedemann (1905, 1906). The blades appear to be longitudinal tabular structures extending the length of the endosiphuncle. The dark peripheral band which they often join was identified by Ruedemann as the endosipholining. As this structure is found in cephalopods in which there is no demonstrable lining extending forward around the speiss and cylinder, his interpretation is open to question.

The appearance of the blades in cross section varies widely. Some types are shown in Text-fig. 2I–P. Text-fig. 21 shows the tip of a triangular cone with three blades, found in a Canadian genus yet to be described; J represents the condition found in *Proterocameroceras brainerdi;* K represents the blades and a compressed cuneate tube characteristic of *Vaginoceras*, sensu stricto; L represents the structure of *Coreanoceras* and some related genera show only slight modifications of this pattern; O and P represent sections at different points in *Meniscoceras.*

The pattern of the blades has been found highly characteristic of certain Canadian genera in the El Paso limestone, where they are conspicuous features of both fresh and weathered cross sections. As such, they have proved useful and convenient horizon indices in the field.

The number and arrangement of the blades may be uniform through the length of the endosiphuncle. In some endoceroids there is unquestionably a marked variation from early to late stages which clearly marks an ontogenetic progression. A Canadian genus now awaiting description has a pair of dorso-lateral blades which move in ontogeny from a dorsal to a relatively lateral position.

Often the blades are well displayed in apical parts of siphuncles where the margins of the cones are not visible. As they are traced orad by cross sections, parts of the cross sections of the cones are first apparent only where they intersect the blades (Ruedemann, 1905). Adorally the cone surfaces may be clear and the blades may become obscure. This is in part recrystalization, but study of numerous sections indicates that conditions of recrystalization are inadequate to account for this phenomenon completely. It is therefore believed that the blades are features which may sometimes characterize early growth stages of the endosiphuncles, and may fade and disappear in later stages. This is certainly true in part of *Proterocameroceras;* it is necessary to explain similar phenomena in some specimens of *Vaginoceras.*

In some Canadian forms from the El Paso limestone there is certainly an adoral disappearance of the blades which must be original and organic. This problem will be discussed in more detail in connection with the description of these forms.

Quite probably all of the radial structures observed in cross sections are not identical in structure or function. In *Hudsonoceras*, described below, two prominent bands, termed primary blades, bound the

ventral mass of the siphuncle. Similar bands have been noted in *Coreanoceras* and *Meniscoceras*. In addition, fainter radial markings are present in *Hudsonoceras* which are not visible in every section, but these structures, called secondary blades because of their fainter appearance, may well be the homologues of the blades found in most other endoceroids. If so, the primary blades represent only a boundary between the prominent thickened mass on one side of the siphuncle and the more normal endocone pattern found on the other. The dark band connecting the multiple tubes of *Allotrioceras*, and the similar circular band connecting the tubes of *Mirabiloceras*, are plainly homologous with each other, but probably not with the radial blades of the other endoceroids.

Hudsonoceras shows a feature not as yet observed in other endoceroids. There are faint bands, darker than the remainder of the endosiphuncle, normal to its axis. Our sections suggest that it is in cross sections which coincide with these bands that the secondary blades are displayed.

Typical blades pass without interruption from the periphery of the endosiphuncle toward the cavity in the center, whether it be a cone or a tube where the section is cut. Ruedemann (1905) however, has figured somewhat different structures in *Cassinoceras explanator*. Here individual radial elements are seen between successive endocone surfaces, varying widely in number and position from one conical element to the next. These structures Ruedemann named endosiphofunicles. As yet, no funicles of this sort have been recognized in any other endoceroid.

Assuredly, the patterns displayed by variations in the form of the endocones, position of their tips, position and form of the tube, number and arrangement of the blades, present an almost bewildering diversity of structure. Some fifteen years of observation of these features has indicated that they are characteristic within a species, though ontogenetic changes as well as vicissitudes of preservation must be taken into account. As such, they serve as valuable taxonomic criteria within endoceroids and, meagre as the present data are, they indicate that they characterize genera having great faunal and stratigraphic significance.

DEPOSITION OF ENDOSIPHUNCLE

From certain essential phenomena of growth it is possible to deduce something of the manner of deposition of the endocones, and to hazard some guesses concerning the function of some of their parts. First some of the essential features will be summarized.

1. The hydrostatic function of the endocone requires that its growth be considerably delayed beyond that of the phragmocone.

2. The endocone grows by the accretion of individual units of fairly uniform thickness, their surfaces are bounded by dark lines.

3. Rapid growth of the early parts of the endosiphuncle is suggested by the faint nature or complete absence of endocones in those portions. Recrystallization is inadequate to account for this phenomenon completely, though it may exaggerate it, and could alone produce the same end result. It fails to account for the disappearance of cones where blades and tubes are clearly displayed. Further, recrystallization is often at its greatest in the centers of large endocones, necessarily late stages. The loss of endocones is greatest just where it would not be expected, from inorganic causes, in the small apical portions of siphuncles.

4. Even with advanced recrystallization, the tubes are often preserved, and retain their identity as tubes with dark definite walls, even though there may be only white calcite bounding them both internally and externally.

5. The blades are only dark longitudinal bands within the endosiphuncle. They never exhibit tubular structures, passing from the tube to the siphuncle wall.

6. Blades are well developed in advanced holochoanitic forms in which invagination of necks and rings is of such a nature that an exchange of materials between the tissues of the siphuncle and those of the camerae is extremely difficult and necessarily indirect; perhaps impossible. No other connection, by possible perforations in the siphuncle wall, has been found.

7. Study of the surfaces of silicified endocones fails to show any modification of the surfaces caused by the juncture of the blades with the endocone surface.

From these facts it is possible to deduce something of the manner in which the endocone was formed. The first and most important question is this: Is the endosiphocone secreted by a mantle surface upon the tip of a siphonal strand which retreats forward in the siphuncle as the endosiphuncle grows, or is it actually the result of deposition of calcite within the siphonal tissues?

Individual conical units show faint growth lines within, but never lamellae normal to the growth lines, such as have been observed in many structures secreted by mantles, including the cameral deposits. This fact suggests but does not prove secretion within tissues.

The endotubes seem functionless as tubes connecting the siphonal strand with the shell apex, which is implied if the cones are a mantle secretion. However, they are more logically interpreted as siphonal structures preserved as calcification of the tissues advances.

The blades are plainly not structures analogous to the radial tubes of the actinoceroids; they are never tubular. They can be logically explained best as slight differentiation and discoloration of calcareous material filling the siphonal tissues, located at regions where this tissue was strengthened to support the endotube, and to maintain it in a normal and regular position in a tissue which was otherwise probably very soft, and which may well have contained large areas of haemocoel. Certainly, any tissue which was so active in secreting calcium carbonate, whether within or outside of itself, must have been very abundantly supplied with blood. It must be remembered that the endosiphuncles sometimes equal or surpass the entire remainder of the shell in mass and weight.

If the blades are shadows, figuratively, of supporting structures in the solid endocone secreted by a mantle, some indication of them should be found on exposed surfaces of the last endocones. No such markings have been found. If, however, endocones are deposited in tissues, the shadows of supporting structures may cause differentiation of color or texture without causing any modification of the endocone surfaces.

It has been suggested that early stages of the siphuncles may have exhibited rapid, essentially uninterrupted growth of the endosiphocone, for which reason boundaries of endocones representing resting stages of growth, are commonly absent there. If this is true, it would be in those early stages that the siphonal tissue would require a great supply of blood. In *Allotrioceras* the multiple tubes of the early stages suggest a specialized means by which this need could be supplied. It is worthy of note that in *Mirabiloceras*, where multiple tubes are preserved to a late stage, growth of the endocones was apparently essentially continuous also, and perhaps even rapid, for margins of individual conical elements are visible neither in cross nor longitudinal sections. It is suggested that *Mirabiloceras* may have been a shell in which the entire growth was extremely rapid, or that the endocones appeared late and then grew very rapidly to maintain the usual hydrostatic balance of adult shells. Which possibility is true can, of course, only be determined when *Mirabiloceras* is known from more nearly complete material, preferably a suite of complete shells representing different growth stages. The possibility of obtaining such material is unfortunately remote.

EVOLUTION AND CLASSIFICATION

The first endoceroids appear in the middle Canadian. They agree with the Ellesmeroceratidae of the lower Canadian, doubtless their ancestors, in the form of the apical portion of the shell and the structure of the wall of the siphuncle. They differ fundamentally from the ellesmeroceroids in lacking diaphragms crossing the siphuncle, and possess instead a solid endosiphuncle composed primarily of endocones. Other differences, though useful in field identification, are relatively superficial. The first endoceroids are slender shells, but differ from the slender ellesmeroceroids in their much larger size. The cross section of the shell is broader, generally slightly depressed in section, though *Pachendoceras* of the Ellesmeroceratidae is depressed also, and

Cotteroceras of the endoceroids is compressed.

This is the fundamental pattern of the oldest and most primitive of the Endoceratida, the family Proterocameroceratidae (see Flower, 1947, Flower and Kummel, 1950). Within this family various specializations occur. Most prominent among them, are those pertaining to the endosiphuncle. The simpler genera have relatively simple cones, terminating in a relatively central tube. Sections of many of these forms have thus far failed to demonstrate clear endosiphoblades, which may well be a later specialization. However, it is within this family that specializations occur. The tip of the cone may come to lie close to either the dorsal or ventral margin. One side may be flattened, grooved, or slighly concave. Unfortunately little attention was given to these features in the recent description of Canadian endoceroids (Ulrich, Foerste, Miller and Unklesbay, 1944), but much information has been accumulated since that time which will be presented in detail elsewhere. *Proterocameroceras*, the internal structure of which was made known by Ruedemann (1905), is highly specialized internally.

Within this family there is also specialization of the siphuncle wall. The necks of *Proendoceras*, defined below, are short and simple in the young, where the connecting ring shows no clear structural differentiation. Later stages of the same form show a gradual elongation of the necks, a thickening of the connecting ring, and a transition between the layered ring, believed to be primitive, and the eyelet type; the original inner layer tends to become thickened and eventually concentrated at the tip of the ring, thus being modified into the eyelet of more advanced endoceroids. Similar elongation of the necks appears to be present in *Clitendoceras*.

In this connection, it should be noted that Teichert and Glenister (1954) have regarded three endoceroids from the Canadian of Australia as belonging to the more advanced Endoceratidae. One of these, *Cyrtendoceras carnegei*, I regard not as a true *Cyrtendoceras*, but as the adoral part of a piloceroid. The second genus, *Lobendoceras*, has calcite within the siphuncle, but not clear endocones. The calcite may well, from the present evidence, be inorganic; if so, this genus is assignable not to the endoceroids, but instead to the family Thylacoceratidae of the Ellesmeroceratida. The third genus and species, *Campendoceras gracile*, is a true endoceroid, in which the necks are subholochoanitic, that is, almost but not quite reaching to the preceding septum; it lies within the anticipated limits of the Proterocameroceratidae. It should be noted also that while the genotype of *Pachendoceras* is not an endoceroid, two middle Canadian species probably are, and are to be referred instead to the new genus *Proendoceras*. They are *Pachendoceras newportense* and *P.? sayi*. These matters are noted here as they might otherwise seem to oppose the concept that as far as known, the slender endoceroids of the Canadian belong to the Proterocameroceratidae and not to the Endoceratidae.

The piloceroids are a new development in the Canadian, doubtless stemming from the Proterocameroceratidae. They differ in the short rapidly expanding shells and the widely expanding siphuncles. They are the only endoceroids so far found in the Canadian which have attained truly holochoanitic septal necks. These features are shown in both *Piloceras* and *Cassinoceras*, genera which are dominant in the later Canadian, largely in the equivalents of the cotter and younger beds. The piloceroids occur earlier in the El Paso limestone, in the portion regarded as the equivalent of the upper half of the Gorman formation of Texas, and the supposed equivalent of the Roubidoux formation of the Ozarks and the *Lecanospira*-bearing beds of the eastern sections. The situation thus presented is seemingly anomalous. The middle Canadian beds of the east contained a relatively primitive cephalopod association, with the Proterocameroceratidae and Basslerocera-tidae; the supposed western equivalents had the Basslerocera tidae poorly developed, but contained Proterocameroceratidae of a seemingly more advanced type, joined by the Piloceratidae and Tarphyceratidae which appear only later in the eastern sequence. Closer analysis leads, however, to the belief that this difference is largely due not to different faunal realms, but to a slightly earlier age of the eastern beds. The basis of this interpretation will be discussed

in detail elsewhere; it will suffice to point out here that the cephalopod types actually precede the occurrence of *Lecanospira* very slightly in eastern New York.

Piloceroids are generally recognized on the gross features of the shell, the very rapid expansion of both the siphuncle and the phragmocone. Siphuncles are so broad as to leave but a relatively small proportion of the phragmocone space for the camerae. Adorally, however, both the shell and siphuncle may become markedly more slender; sometimes the living chambers are slightly contracted at the apertures. Often the adoral part of the siphuncle is rather abruptly constricted, the cameral space being proportionately increased. Shells vary in curvature; they are typically slightly curved, and endogastric as are all known curved endoceroids. One form, now awaiting description is gyroconic, as strongly curved as is *Cyrtendoceras* of the upper grey *Orthoceras* limestone of Sweden. Others, largely those grouped at present in *Allopiloceras*, are straight or nearly so. Fuller discussion of the group will accompany the description of the piloceroids of the El Paso limestone, a study which is now well advanced.

It is evident at the present time that the piloceroids as a form group are complex and diverse. Some genera currently grouped as piloceroids have nothing to do with the true Piloceratidae. *Coreanoceras* is, in the opinion of the writer, a member of the Proterocameroceratidae. The large, rapidly expanding genera of the Asiatic Canadian, *Manchuroceras* and *Chihlioceras*, exhibit specialized endosiphuncles and may well be derived independently from some other branch of the Proterocameroceratidae.

The true Endoceratidae make their first appearance in the Chazyan and range to the Richmond. Two points of similarity indicate that they arose, not from the Proterocameroceratidae which they resemble externally, but from the Piloceratidae. They agree with the Piloceratidae in the structure of the wall of the siphuncle. The early stage known as the genus *Nanno* cannot be explained adequately as a recapitulation of a preseptal phase. It is now evident that no such recapitulation is found in strata older than the Chazyan. Instead, it is a recapitulation in the early stages of the Endoceratidae, of the rapidly expanding siphuncles, and also shells, of the true Piloceratidae. In some younger and more specialized endoceroids tachygenesis causes this recapitulatory stage to be reduced and eventually lost. The first step is the enclosure of the swollen apical end of the siphuncle in camerae, found in *Suecoceras*. The swelling of the siphuncle is further reduced in *Cameroceras*, and even this slight swelling is eventually eliminated in the apical end to which the generic name *Foerstellites* Kobayashi has been given.

It is not unnatural, in view of the very incomplete state of our knowledge of many endoceroids, that there are many genera which cannot be placed anywhere in this scheme with certainty. Careful restudy of many of the described genera is still required. The features of the endosiphuncle are unknown for many of the genera based upon species showing the gross features of the phragmocones. Other genera are based upon species as yet known only from isolated endosiphuncles. There are many genera in both groups for which the wall structure of the siphuncle is unknown. Prior to 1941 it was supposed that all endoceroids were holochoanitic. No efforts were made to ascertain the wall structure by means of sections, and very little has been done since.

With the exception of some Chazyan species, all of the endoceroids of Chazyan to Richmond age are holochoanitic and members of the Endoceratidae. Among the Chazyan species are some with short necks; they are plainly unrelated to the Endoceratidae, and are derivatives of the Proterocameroceratidae. They further agree with the Proterocameroceratidae and differ from all previously known Endoceratidae in possessing a very complex organization of the endosiphuncle. Is it possible that among such endoceroids there may be some which retain the complex endosiphuncles of the specialized Proterocameroceratidae, but which also parallel the development of the Piloceratidae and Endoceratidae in the extreme elongation of the septal necks? Such a possibility is suggested by the genus *Hudsonoceras* described below. Empirically, one may take one's choice here. One could, on the basis of the close similarity of the endosiphuncles, insist that this genus is a

derivative of *Coreanoceras*, and therefore stems from the Proterocameroceratidae. One could, on the other hand, maintain that homeomorphy has produced in the Endoceratidae an endosiphuncle very similar to that of the unrelated *Coreanoceras*. The former interpretation is believed to be the true one. Within the older Proterocameroceratidae there is already evident a tendency toward elongation of the septal necks. It may well have attained or even surpassed the holochoanitic condition by Chazyan time, quite independent of the Piloceratidae and Endoceratidae. The placing of *Hudsonoceras* with the Endoceratidae requires the admission that nowhere in that family is there another form known which even remotely approaches *Hudsonoceras* in the complexity of the endosiphuncle.

A dilemma is presented by attempting to include a macrochoanitic form like *Hudsonoceras* in the Proterocameroceratidae, where the necks are typically too short to be called holochoanitic. Probably the best solution is the recognition of another family group to include derived Proterocameroceratidae with such specialized siphuncles, within which extreme elongation of the septal necks may be another specialization. Tentatively, the family Manchuroceratidae is employed for such endoceroids, though many problems beset its definition and proper scope, and some questions of priority and nomenclature are also involved in the use of the name.

The family Allotrioceratidae described below is so utterly strange that one is tempted to define it in the terms which Barrande first used in connection with *Ascoceras*, and which some claim constitute a description and validation of the name: "très bizarre." The only endoceroid which seems to be even remotely possible as an ancestor of this family is the genus *Meniscoceras*. By its short necks and specialized endosiphuncle *Meniscoceras* is a specialized derivative of the Proterocameroceratidae, not of the Endoceratidae. The evidence is incomplete and admittedly ambiguous, but does suggest strongly that in *Mirabiloceras* at least there may well be another independent development of septal necks long enough to be called holochoanitic or even macrochoanitic.

It is necessary to close the discussion of the phylogeny and classification of the endoceroids with a review of some of these uncertainties, for until much more morphological evidence is available there will remain much uncertainty as to the relationships of many of these stranger genera of endoceroids. The problem is particularly acute in relation to some genera based upon material from eastern Asia, the morphology of which is only incompletely known at the present time. More and better material is needed for these genera, and the possibility of obtaining it is sadly remote.

It seems pertinent, however, to attempt to clear the air for a fuller investigation by making known some facts which have remained too long unrecorded, by recording the structures of the type species of some long used—and misused—genera, and by describing some new forms exhibiting some remarkable structures. Emphasis in this respect is placed upon post-Canadian genera. New material from the rich cephalopod faunas of the El Paso limestone promises to contribute so much new information concerning the Canadian genera and species, that it seems pointless to attempt here more than the proposal of one generic group, the need of which has long been felt, and a brief summary of the known features of the genera and a listing of those features which are yet unknown.

DESCRIPTION OF GENERA AND SPECIES

Note.—Under this heading are grouped together descriptions and discussions of some previously described genera, the restudy of which has been rewarded by enough information to justify formal redefinition. Some genera are thus redefined and made useful. It has been concluded that some other generic names cannot be employed profitably, and may well remain as genera dubia. There are included here some new generic groups, accompanied in most cases by a description of the species upon which they are based.

Genus ENDOCERAS Hall, 1847
Genotype: *Endoceras proteiforme* Hall, 1847

Many vicissitudes surround the use of the name *Endoceras*, which has become com-

monly accepted as the genus typical of the group which today constitutes the order Endoceratida. Citations of the genus are so numerous that no synonomy has been included here. Bassler (1915) indicates that the first use of the name was Hall, 1844, Am. Jour. Sci., Arts, vol, 47, p. 109. No species was described at that date, and for purposes of nomenclature the genus first became available when Hall described it in 1847 on page 58 of the first volume of the Paleontology of New York. It is more fully discussed in a footnote on page 207 of the same work. So far as I am aware, there has been no formal designation of a genolectotype. I therefore designate *Endoceras proteiforme* Hall as the selected genotype of *Endoceras*.

Other generic names have been proposed for endoceroids prior to Hall's valid proposal of *Endoceras* but are based upon fragmentary and poorly preserved specimens. One can recognize that the type species are endoceroids, but little more can be determined about them. Of these names, *Cameroceras* is discussed below. The other generic names, *Sidemina* Castlenau, 1843, *Sannionites* Fischer de Waldheim, 1829, and *Conoceras* Bronn, 1835, are based upon species which can be recognized as fragments of endoceroids, but nothing further can be determined about them. Should their type species ever be reaffirmed by a study of type and topotype material, it should be urged that a suspension of the rules of nomenclature be requested for the retention of *Endoceras*. There are also other generic names, *Diploceras* Conrad, 1842, and *Colpoceras* Hall, 1850, based upon inadequately known endoceroids, which would not affect the legal retention of the generic name *Endoceras*.

As at present understood, *Endoceras* is a rather broad genus, ranging in age from the Chazyan through the Richmondian. Canadian species which have been assigned to *Endoceras* certainly do not belong to that genus. Many of them have been placed elsewhere by Ulrich, Foerste, Miller and Unklesbay (1944). Some endoceroids of generalized aspect were left in *Endoceras* by these authors. What is known of these species and their proper generic assignment is indicated below.

Endoceras proteiforme is one of several species of *Endoceras* recognized by Hall from the Trenton limestone of Trenton Falls, New York. These specimens unquestionably came from the Denmark member of the Sherman Fall limestone of the Trenton. Study of some type and much topotype material indicates that the following characters apply to *Endoceras*.

Shells large, straight, externally relatively smooth. Cross section very slightly wider than high in the mature portion, but compressed in cross section in the young. Sutures are straight and transverse. Siphuncle close to the ventral wall of the shell, segments definitely concave between the septa in the young, but often tubular in outline in the adult. Siphuncle wall composed of holochoanitic necks and connecting rings, as illustrated by Hyatt (1900, p. 515, fig. 1056). Endosiphuncle composed of endocones, which in the type species are not particularly short or widely spaced. In topotype material which I regard as typical, the speiss is circular in cross section, but terminates in a tube at least twice as close to the ventral wall as to the dorsal wall (Text-fig. 2N). Blades are not clearly preserved in the typical material I have examined, but most endosiphuncles from the Denmark member are rather coarsely recrystallized.

As at present understood, *Endoceras* ranges from the Chazyan to Richmondian. It includes species showing the features of the septa and siphuncle wall of the above description. It includes shells showing wide variation in the shape of the endocones and position of the tube. There is indication also that there is variation in the number and position of the blades. Cones of circular and depressed oval sections are known; some are triangular with the apex directed downward (Text-fig. 2J) while a group of specimens from the Eden or lowermost Maysville of the Cincinnati region is characterized by triangular endocones, the apex of the triangular cross section directed upward (Text-fig. 2M).

While the early stages of typical *Endoceras* are of the type to which the name *Cameroceras trentonense* has been applied in the past, it is fairly certain that the early stages of some of the large Platteville species are *Nanno aulema*, and the early portion of a

large *Endoceras* from the Saluda beds, were *Endoceras faberi* Foerste, later made the genotype of *Foerstellites* Kobayashi. For these reasons, serious vexations attend any attempt to subdivide the genus *Endoceras*, caused both by the perplexities resulting from the fragmentary nature and poor preservation of much of the material, and from the intricate problems of nomenclature which will inevitably be encountered. There can be no doubt, however, that divisions exist in the genus *Endoceras*, recognizable on the basis of early stages and structure of the endosiphuncle, which are worthy of further attention. Indeed, they supply the only clues by which species can be recognized other than the gross proportions of the shells. Proportions are not useful or reliable features in endoceroids. The extent of variation in original proportions within a species is not known. Original proportions are often greatly modified by flattening accompanying compaction of sediments.

Canadian species formerly assigned to *Endoceras*

While there may be a basis for some difference of opinion as to what constitutes the genus *Endoceras*, there can be no doubt but that it is a straight smooth cephalopod with a large siphuncle located close to or in contact with the ventral side of the shell, and that the septal necks are as long as the segment of the siphuncle, and are supplemented by connecting rings which extend from the tip of one neck apicad to that of the next. The siphuncle contains endocones which, until the genus is more closely delimited, may show some variation in cross section.

Defined in these terms, *Endoceras*, while still a very broad genus, is not known from beds older than the Chazyan. Yet a large number of Canadian species have been referred to *Endoceras* by Ulrich, Foerste, Miller and Unklesbay (1944). A review of these species shows that they are largely inadequately known, but that in no single case is there evidence of the long septal necks which characterize the Endoceratidae. Instead, many of these forms which have been assigned to *Endoceras* belong to the Proterocameroceratidae. A few are so inadequately known that it is not certain whether or not they are endoceroids, and a few are definitely members of the Ellesmeroceratidae, Baltoceratidae and Basslerocera-tidae, and are not endoceroids at all.

Endoceras? annuliferum (Flower). Ulrich et al. refer this species to *Endoceras* with question, a change of very dubious merit. The species is here made the genotype of the new genus *Proendoceras*. The form is a generalized one, of circular or slightly depressed cross section, and sutures which are straight and transverse or nearly so. The species is from the middle Canadian which, now under restudy, reveals much in common among the materials at Beekmantown, described from the Kirby ledge, the Ticonderoga material, abundant materials from Fort Ann, New York, and also the Rochdale limestone of southeastern New York. Specific relationships in the group are complex, but the identity of *Endoceras wappingerense*, *E. warthini*, *E. champlainense*, and possibly several others, must be considered.

Endoceras? aristides (Billings). Ulrich et al. (1944, p. 92, pl. 47, fig. 7) have referred this from to *Endoceras*. Billings had placed it in *Cyrtoceras*. The holotype, from the Naylor ledge limestone at Phillipsburg, Quebec, is identical in appearance with many specimens of *Basslerоceras* which I have encountered, and is very similar to some in the middle Canadian at Fort Ann and at Rochdale. The species is thus far known only from the type, showing a somewhat oblique weathered section. We cannot refer any other specimens to this species with certainty, though this may eventually be remedied by the study of topotype material.

Endoceras? baculoides (Blake). This is based upon an isolated siphuncle from the Durness limestone of Scotland. The siphuncle is larger than that of an ellesmeroceroid, and is probably that of an endoceroid, but its position within the Endoceratida cannot be ascertained until its structure is better known.

Endoceras? baylorense Ulrich et al. (1944, p. 93, pl. 42, fig. 1–5), is based upon a siphuncle with oblique annular markings on its surface. The siphuncle is slightly depressed, and is regarded as being in contact with the ventral wall of the shell. Endocones are semicircular in section. There is no

evidence as to the condition of the length of the septal necks. The species is so close to *Proterocameroceras* that I tentatively assign it to that genus. It occurs in El Paso limestone, and is characteristic of beds correlated with the Jefferson City.

Endoceras? calvini Ulrich et al. (1944, pl. 49, fig. 6), from the Oneota dolomite of Iowa, is, from the extant features, more probably an unusually large *Ellesmeroceras* or *Eremoceras* than an endoceroid.

Endoceras? champlainense Ruedemann (1906) is based upon a series of rather poorly preserved specimens from the middle Canadian near Beekmantown, New York. The original of Ruedemann (pl. 1, fig. 4) is different from the others (pl. 1, fig. 1–3) having much deeper camerae. Siphuncles similar in proportion to pl. 1, fig. 1–3, have been found in a better preserved condition in limestones of the same age at Fort Ann, and have proved to belong to *Proendoceras*.

Endoceras? deparcum (Billings), from the Romaine formation of the Mingan Islands, is known only from a very closely septate fragment of a straight cephalopod, but even the siphuncle is unknown, so it is not certain even that this form is an endoceroid.

Endoceras? durinum (Blake), of the Durness limestone of Scotland, is known only from an isolated siphuncle, having the aspect of an endoceroid.

Endoceras? eburneolum (Stauffer) of the Shakopee dolomite of Minnesota is an othocone with a small submarginal siphuncle. From the size of the siphuncle, the species is not an endoceroid, and its general form has more the aspect of the Baltoceratidae. Further study is required before a generic assignment will be possible.

Endoceras? glaucus (Billings) is based upon one crushed siphuncle, and one phragmocone, most of which has been lost by weathering. It appears to be an endoceroid, but it is doubtful even whether the species can be recognized from other material than the types. It is from the middle Canadian of Grenville County, Ontario.

Endoceras? hageri (Hall) is from the Canadian at West Haven, Vermont. The exact horizon is uncertain, the type apparently can not be located, and the position of the form is very uncertain. It bears cancellate surface markings, unlike those known in any other endoceroid. The siphuncle has not been observed. From the original drawing, the break in the phragmocone should show the siphuncle if this species is an endoceroid.

Endoceras? indigator (Billings) of the Romaine formation of the Mingan Islands, is based upon a series of isolated endoceroid siphuncles, some showing endocones. The nature of the siphuncle wall is unknown.

Endoceras? knighti Ulrich et al. (1944, p. 97, pl. 51, fig. 1) is a long slightly curved siphuncle from the "*Piloceras* bed" of the El Paso limestone. It has an endocone, and is obviously an endoceroid. What little is known of this form leaves it indistinguishable from siphuncles of the genus *Clitendoceras*. It should be noted that the "*Piloceras* bed" of King is the equivalent of the Roubidoux formation, generally considered middle rather than upper Canadian.

Endoceras? lamottense Ulrich et al. (1944, p. 98, pl. 52, fig. 1–3), is from the Chazyan of the Champlain Valley, and is very closely allied to the forms which Ruedemann described as *Vaginoceras oppletum;* indeed from the extant description and figures, as well as my own material, I am not able to distinguish the species.

Endoceras? lawrensense Ulrich et al., (1944, p. 98, pl. 53, fig. 8), is an orthocone from the Levis conglomerate, with unusually deep camerae for a Canadian cephalopod. The siphuncle is large, submarginal. No endocones are known. The form is not demonstrably an endoceroid, nor is it certainly lower Canadian, as was believed by its describers.

Endoceras? logani Ulrich et al. (1944, p. 98, pl. 51, fig. 2–3) also of the Levis conglomerate boulders, is a small shell, closely septate, circular in section, with an unusually large siphuncle. Again, no endocones are known, and it is not certain that it is an endoceroid, nor is its lower Canadian age certain, as the Levis boulders contain some genera otherwise not known below the base of the middle Canadian, notably *Basslerocera*s, and some related genera of the Basslerocerati dae.

Endoceras? phillipsburgense Ulrich et al. (1944, p. 99, pl. 49, fig. 3–4), is based upon a single specimen, showing a weathered surface, apparently slightly curved, and a depressed cross section with a large siphuncle.

The curvature is probably not original. The form may be an endoceroid, or may not. It is difficult to see why it was described from such meagre material. As usual, nothing is known concerning the structure of the wall of the isphuncle. It is from the Naylor Ledge limestone at Phillipsburg, Quebec.

Endoceras? primigenium (Vanuxem) is from the Tribes Hill limestone of New York. Vanuxem's original type cannot be located. Hall figured as this species (1847) some undoubted *Ectenoceras*. On the basis of the original description, the reference to *Orthoceras* is as warranted as the later reference by Ulrich et al., to *Endoceras*. Additional material, which appears to represent this species, from the Tribes Hill limestone, has proved to belong to the genus *Ectenoceras*. No endoceroids have been found in the Tribes Hill limestone.

Endoceras? pusillum (Ruedemann) of the Fort Cassin formation of the Champlain Valley was originally described as a *Baltoceras*. It is based upon an early stage of a cephalopod, sectioned vertically, showing a siphuncle which is marginal to the apex, as is true of the ellesmeroceroids, primitive endoceroids, and the Baltoceratidae. The small siphuncle and the absence of endocones indicate that it is not an endoceroid. I have collected fragments of a much later stage of a typical *Baltoceras* from the same formation. They are probably conspecific with this species, which I regard as a true *Baltoceras*.

Endoceras? richardsoni Ulrich et al. (1944, p. 100, pl. 12, fig. 1–2) is known from a fragment of a relatively large straight circular shell from the boulders of the Levis conglomerate. The siphuncle is marginal, its structure unknown. It is not even certain that this species is an endoceroid.

Endoceras? sansabaense Ulrich et al. (1944, p. 101, pl. 29, fig. 15) The holotype is a siphuncle expanding with moderate rapidity, from a Gasconade horizon of the Ellenberger limestone of Texas. Endocones are not evident. The siphuncle probably belongs to an ellesmeroceroid of the *Eremoceras* persuasion, but the isolated siphuncle alone is hardly worthy of a specific name.

Endoceras? cf. *E.? tenuiseptum* (Hall). Foerste referred this form, from the lower Canadian of Bache Peninsula to *Cameroceras tenuiseptum* provisionally. It is a weathered portion of a rather closely septate phragmocone, apparently compressed in section, and narrowly rounded at one end. I regard it as probably an ellesmeroceroid on the basis of these features, but the form is so incomplete that a definite identification is not possible except in the light of topotype material.

Endoceras? tityrus (Billings), from Phillipsburg, Quebec, horizon uncertain. The type has not been figured and cannot be located. The species cannot be recognized with certainty and its reference to any valid genus is impossible, and indeed, it is rather pointless to even make such an attempt.

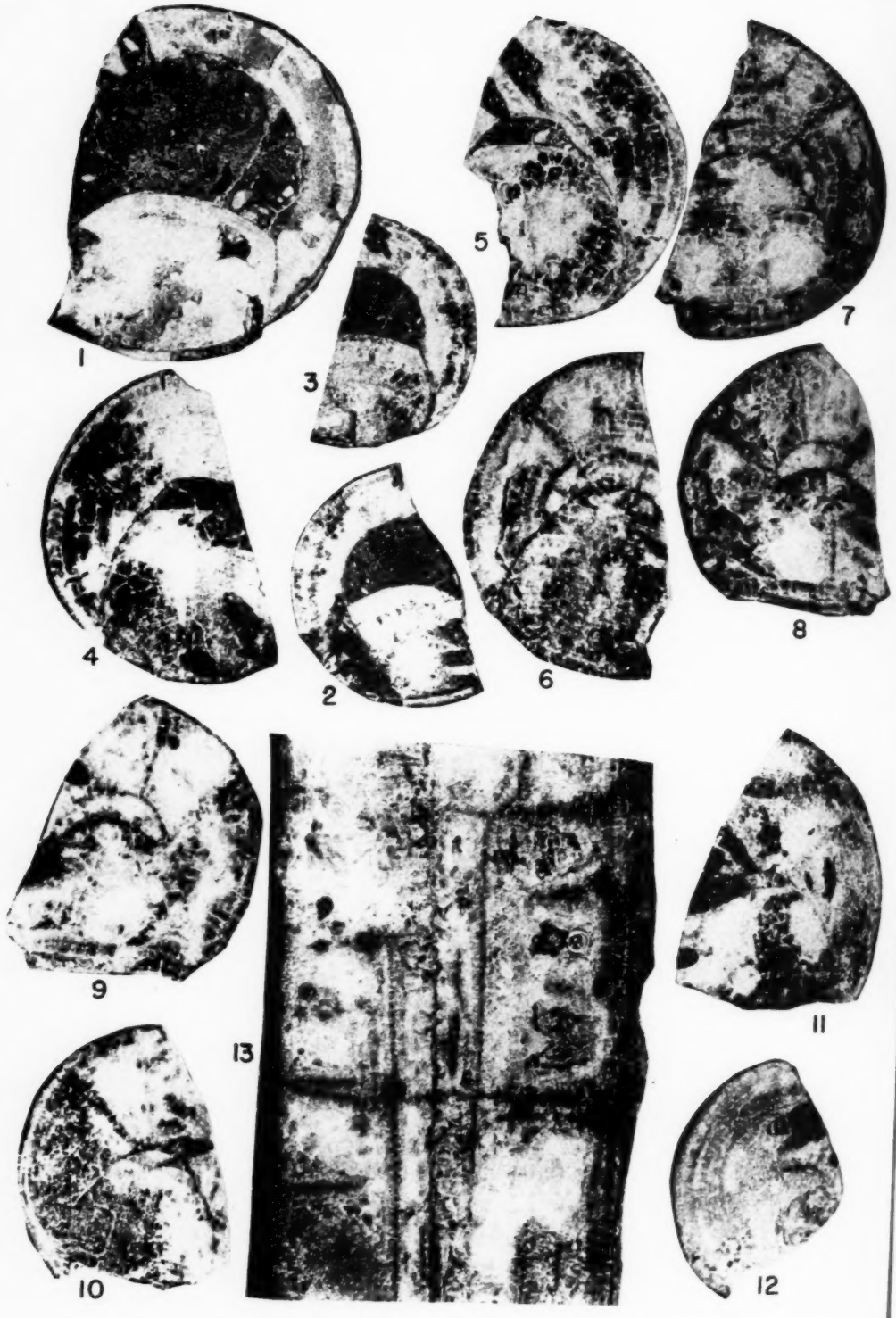
Endoceras? trundlense Ulrich et al. (1944, p. 102, pl. 51, fig. 13–15). This species is based upon endosiphuncles of a large endoceroid, showing endocones. Needless to say, since the siphuncle wall is unknown, the affinities of the form cannot be determined. It is reported as from a Cotter horizon in Tennessee.

Endoceras? wappingerense Ulrich et al.

EXPLANATION OF PLATE 32

FIGS. *1–4—Hudsonoceras aristos* Flower, n. sp., Holotype. *1*, Lateral surface of the entire specimen, 38 cm. in length, sutures slightly retouched. *2*, Composite photograph of cross section of the siphuncle, taken from two mirror images from the same cut, at 3 in fig. 1; about X2.3 natural size. Note growth lines in the ventral mass, and prominent dark bands separating it from the dorsal thinner portion of the endocones. The lower left side is broken, causing the blade to be obscure there. The dark patch just to the right of the center top is a cavity made by some boring organism. *3*, Vertical section through phragmocone, taken just orad of 2 in fig. 1, ×1, showing siphuncle wall, endocones, of which the ventral mass is massive, and extends much farther orad than does the dorsal part of the endosiphuncle. Note straight transverse lines through ventral mass at several points. *4*, Enlargement of part of the dorsal wall of the siphuncle from the same section, about ×4. See also Plate 33. Chazy limestone, bay north of Cystid Point, southeastern shore of Valcour Island, Lake Champlain. (p. 352)

Flower, Endoceroid classification



Flower, Endoceroid classification

(1944, p. 102, pl. 53, fig. 1–5). This is a straight endoceroid of rather generalized aspect, common in the Rochdale limestone of southeastern New York. The section is slightly depressed, the sutures not well shown, but apparently straight and transverse or nearly so. The siphuncle wall is ellipochoanitic, as shown by my own material, and the form belongs to the Proterocameroceratidae, and not to the Endoceratidae. The species is a generalized member of the Proterocameroceratidae, and is here referred to the genus *Proendoceras*.

The Rochdale fauna is more widespread than was previously supposed. It occurs in unnamed middle Canadian near Fort Ann, New York, from which I have abundant material, and extends north in Vermont and New York in the artificial formation which Cady (1945) mapped as the Bascome formation. Unfortunately, the lower Bascome is middle Canadian, and is separated by the appearance of a sandstone from the late upper Canadian, Fort Cassin formation, which comprises its upper part. The specific evaluation of this, and also the next species, is delayed pending a closer restudy of the faunas. It should be noted that *Proendoceras annuliferum* occurs in the same association.

Endoceras? warthini Ulrich et al. (1944, p. 103, pl. 49, fig. 1–2). This species, also from the Rochdale limestone, differs from the preceeding form in proportions. The section is nearly circular, the sutures straight and transverse. Material from Fort Ann, agreeing closely with the type, has shown ellipochoanitic septal necks, and this species is assigned to the genus *Proendoceras*.

Endoceras? yellvillense Ulrich et al. (1944, p. 103, pl. 49, fig. 5). This is a large endoceroid, of apparently straight and transverse sutures, but uncertain cross section. Nothing is known of the structure of the siphuncle wall. Analogy with other Canadian endoceroid leads me to believe that it will prove to be a member of the Proterocameroceratidae, but preservation is such that the nature of the siphuncle wall cannot be proved from the present material. In the light of our present findings, the assumption that it is a member of the Endoceratidae and holochoanitic is not warranted by any other Canadian material. It is from the Powell dolomite of Arkansas.

Endoceras? sp. (1) Ulrich et al. (1944, p. 103, pl. 33, fig. 7). This form is known only from a natural section, vertical or nearly so, showing a straight cephalopod with a marginal siphuncle. From the evidence, it could be an endoceroid or an *Ellesmeroceras*. Collecting on the part of the writer, and also of Mr. Donald Fisher, who is restudying the Tribes Hill formation, has yielded ellesmeroceroids, but not a single endoceroid. I therefore refer this form to *Ellesmeroceras*.

Endoceras? sp. (2) Ulrich et al. (1944, p. 104, pl. 53, fig. 6). Little can be ascertained from the type, which shows again a vertical longitudinal section. This form, on

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EXPLANATION OF PLATE 33

FIGS. *1–13—Hudsonoceras aristos* Flower, n. sp. *1*, Cross section of siphuncle at 2 on Pl. 32, fig. 1, ×2.4. *2*, Same at 3, anterior end of section, note borings in lower right of figure, ×1. *3*, Mirror image of same cut, showing a short vertical line in midventral region, ×1. *4*, cross section 52 mm. farther apicad, showing great reduction of endosiphocone. *5*, Mirror image of same cut, showing borings on upper left, and a slightly smaller cone. *6*, Section 60 mm. apicad, showing extreme tip of cone, and *7*, its mirror image, 3 mm. farther, showing no trace of cone and extremely obscure tube. Note faint blades in the dorsal portion. *8*, Section 40 mm. farther, showing two pairs of dorsolateral blades and a midventral blade. One endocone is greatly darkened, dorsally, and forms an oval with the line of the two primary blades; the ventral side of the cone is obscure. *9*, Mirror image of same, showing variation in clarity of the blades. *10*, Section 22 mm. apicad, with its mirror image, *11*, showing lenticular tube, primary and secondary blades. *12*, Section near apex of specimen, 60 mm. farther apicad, showing tube, and all blades obscurely preserved. *13*, Longitudinal, nearly vertical section, taken between cross sections 7 and 8, showing transverse dark lines, central line of primary blades and tube, and a relatively dark endocone, the dorsal half, only, of which is seen in fig. 8. Same specimen as Plate 1. Except for figs. 2 and 3 which are ×1, all sections are ×2.4. (p. 352)

the basis of other material, I regard as a member of the Proterocameroceratidae, allied to *Proendoceras annuliferum*, *P. wappingerense* and *P. warthini*. It is from the middle Canadian portion of the Beekmantown of Clinton County, New York.

Endoceras? sp. (3) Ulrich et al. (1944, p. 104, pl. 10, fig. 10). This is an isolated endoceroid siphuncle from some part of the section at Phillipsburg, Quebec. Reference to the Hastings Creek formation is tentative. It cannot be told whether the siphuncle belongs to the Proterocameroceratidae, as we suppose from its position in the Canadian, or to the Endoceratidae.

Endoceras? sp. (4) (Ulrich et al., 1944, p. 104). This specimen, the only large orthoceracone from the Manitou dolomite, is of uncertain position. Its siphuncle has not been observed.

Endoceras? sp. (5) (Ulrich et al., 1944, p. 105). This form, from the Baswood Creek limestone, is an orthocone with a marginal siphuncle. What little is known of it is consistent with placing it either in the Proterocameroceratidae or the Endoceratidae. Even its nature as an endoceroid could be questioned, for no endocones are reported.

Endoceras? sp. (6) This is another inadequately known form, this time from St. John, New Brunswick. The figured specimen of Matthew could not be located.

Genus CAMEROCERAS Conrad

Genotype: *Cameroceras trentonense* Conrad.

Cameroceras CONRAD, 1842, Philadelphia Acad. Nat. Sci., Jour., vol. 8, p. 267. ——, HALL, 1847, Paleontology of New York, vol. 1, p. 198, p. 221. ——, D'ORBIGNY, 1849, Prodrome de Paleontologie, vol. 1, 2nd, ed., p. 642. ——, SAEMAN, 1852, Paleontographica, vol. 3, p. 162. ——, PICTET, 1854, Traité de Paleontologie, 2nd ed., p. 642. ——, EMMONS, 1855, American Geology, vol. 1, pt. 2, p. 148. ——, SALTER, 1859, Geol. Soc. London, Quart. Jour., vol. 15, p. 376, fig. 2. ——, BARRANDE, 1874, Système Silurien du centre de la Bohême, vol. 2, part 3, p. 782. ——, WHITFIELD, 1882, Geology of Wisconsin, vol. 4, p. 228. ——, MILLER, 1889, North American Geology and Paleontology p. 432. ——, CLARKE, 1897, Geology of Minnesota, vol. 3, pt. 2, p. 775. ——, HYATT, 1900, Cephalopoda, in Zittel, Eastman Textbook of Paleontology, vol. 1, 1st. ed., p. 514; reprinted in later editions with different pagination. ——, RUEDEMANN, 1906, New York State Museum, Bull. 90, p. 404. ——, GRABAU & SHIMER, 1910, North American Index Fossils, vol. 2, p. 39. ——, FOERSTE, 1924, Denison Univ. Bull., Sci. Lab., Jour., vol. 20, p. 212. ——, SARDESON, 1925, Pan American Geologist, vol. 43, p. 185 ff. ——, FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., vol. 22, p. 29. ——, FOERSTE, ibid., vol. 24, p. 155. ——, SARDESON, 1930, Pan American Geologist, vol. 53, pp. 175–182. ——, ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, Geol. Soc. America, Special Paper 58, p. 106.

This generic name has been widely employed for American, European and Asiatic endoceroids, but definitions of the genus are relatively few, and there is much cause to wonder what the precise concepts of the genus may have been among various authors. Sardeson (1930) has summarized the definitions of this and of some related genera and has raised the very significant question as to whether the genotypes of *Cameroceras* and *Endoceras* may not be different growth stages of the same true species. If so, *Endoceras* must certainly be suppressed as a synonym of *Cameroceras*, by simple application of the rules of priority. Sardeson has presented a convincing case but has failed to consider the structure of the ecto- or endosiphuncles, and seems to have based many of his observations upon Minnesota material which may, or may not, be conspecific with *Endoceras proteiforme* as he assumes. These omissions, naturally, greatly weaken his argument.

It is evident that there has been no uniformity in the distinctions accepted as serving to separate *Endoceras* and *Cameroceras*. Hall (1847) recognized *Cameroceras* and its genotype, but placed all other endoceroids in the then new genus *Endoceras*.

Conrad's description is quoted below:

> Straight, siphuncle marginal; a longitudinal septum forming a roll or involution with the margin of the siphuncle.
>
> This singular genus is confined to the Trenton limestone (Lower Silurian). The shell from which the description is taken resembles an *Orthoceras* externally, but is contracted at intervals; the siphuncle is obliquely undulated, and joins the margin.
>
> Cameroceras Trentonensis. Pl. 16, fig. 3.
>
> *Locality.* Near Middleville, Herkimer county, New York."

Hall (1897, p. 221,) described *Cameroceras* as follows:

> *Character.* "Straight; siphuncle marginal; a longitudinal septum, forming a roll or involution with the margin of the siphuncle."

> The above description is quoted from Mr. Conrad (Jour. Acad. Nat. Sci. Philadelphia, 1842, Vol. viii, p. 267); and although dissenting from his opinion of the characters in part, I have adopted it as a distinct genus, closely allied to *Endoceras*. There is no evidence of a longitudinal septum as described above, in the specimens I have examined; nor is it probable that such a character exists. The character of the siphuncle, though resembling that of *Endoceras*, is different from any examined.

Hall later (1879, p. 227) lists *Cameroceras* with *Colpoceras* and *Nothoceras* as synonyms of *Endoceras*. Hyatt (1884) regarded *Cameroceras* as a synonym of *Sannionites* Fischer de Waldheim, 1837, which he diagnoses:

> Shell has only one thick walled sheath, in connection with the living chamber, not continuous with the funnel of the last septum. The funnels close the interval between the septa as in *Endoceras*, but the siphon is lined by an inner, thick, continuous layer of shell, which is composed apparently of the unresorbed parts of the successive sheaths. Endosiphon is present, but only preserved in a fragmentary way, and often absent in the fossils.

Later (1900) Hyatt lists *Cameroceras* as a valid genus with *Sannionites* and *Suecoceras* as synonyms. No definition is given.

Barrande (1874) quotes Hall's description, notes that *Cameroceras* can be recognized on the basis of the compressed section and the constrictions of the siphuncle, but concludes that these characters are of little importance and that the genus should be regarded as a synonym of *Endoceras*. If the genera are identical, the rule of priority requires the suppression of *Endoceras*, not *Cameroceras*.

Ruedemann (1905) used *Cameroceras* in the broad sense saying: "We use here the older term *Cameroceras* not differentiating between *Cameroceras* and *Endoceras* as Hyatt has done." However, in 1906, Ruedemann recognized *Cameroceras* as characterized by the "one large thick walled sheath" which he interprets to be a final endocone. The one sheath represents to him a final gerontic cone which is often stronger than the others. More stress, however, is laid upon the presence of the endosipholining in *Cameroceras* and its absence in *Endoceras*, a feature not corroborated by the present study.

Foerste (1924) distinguished *Cameroceras* from *Endoceras* by its endocones which he interprets as short, and rapidly tapering and vertically oblique, so that the tip of the cone lies close to the ventral wall of the siphuncle. Unfortunately, re-examination of the specimens leads the writer to accept the criticism of Sardeson (1930) that the peculiar features of the siphuncle are those to be expected in early stages of the ectosiphuncle and have no relation to endocones. Foerste (1924, pl. 24) figures a considerable series of specimens. One is an isolated tip of a siphuncle shown in section, remarkable mainly in that it shows an annulated speiss within an endocone, a condition which has been exaggerated by retouching.

Cameroceras has been interpreted as the apical end of *Endoceras* by Sardeson (1925). His argument is weakened by the fact that he maintains that *Cameroceras trentonense* is the early stage of *Endoceras annulatum*, which is not an *Endoceras*, but the genotype of *Cyclendoceras*. Further, Sardeson's material is not typical, but is from the Middle Ordovician of Minnesota. It remains for a much closer study to determine the specific relations between the endoceroids of these two distant regions. However, Sardeson has presented one point worthy of consideration, namely that *Cameroceras trentonense* is recognized only from early growth stages. On the basis of gross characters, it is possible that later stages have been identified as some species of *Endoceras*. The writer doubts, however, that they are *Endoceras annulatum*. The annular exterior mentioned by Conrad himself is more likely to be the sort of constriction which appears locally in the early stage of *Nanno noveboracum* Ruedemann (Flower, 1941, pl. 3, fig. 5) and does not imply a uniformly annulated ephebic exterior. Such a constriction followed by a relatively smooth shell has been figured (Ulrich, Foerste, Miller and Unklesbay, 1944, pl. 47, fig. 4). Probably the nepionic line of many nautilicones is an analogous structure. The compressed section is a feature which is to be found in the early stages of a number of endoceroids which later in life are depressed or circular, and is probably not significant. Similar compressed early stages have been figured by Holm, on the basis of Swedish material, and have been found from the Chazyan to the Cincinnatian.

The constriction of the siphuncle between the septa fails to supply any good criterion. This feature is variable among species, and even among parts of the same species under different conditions of preservation and also varies from one growth stage to another. The prominence of the last endocone is a feature which this genus shares with members of both *Endoceras* and *Vaginoceras*, as formerly interpreted. The endosipholining is not demonstrated as yet in the genotype of *Cameroceras*. My own observations fail to show any such organic structure in topotype material. It therefore cannot be used as a criterion of the genus in the present state of our knowledge. Indeed, it is to be feared that the endosipholining is in a large part at least an inorganic replacement phenomenon. The marginal siphuncle and compressed section seem to have little value. The oblique and short endocones used by Foerste seem to be a misinterpretation of structures connected not with the endocones but with the apex of the siphuncle. In short, none of the previously used criteria supply any good basis for differentiating *Cameroceras* generically from *Endoceras*.

The specimens currently included under *Cameroceras trentonense* show a wide variation in proportion, indicating either a high degree of variability, or that several species have been included under that name. The specimens all represent apical portions of shells. They come from the middle Trenton, (Denmark member of the Sherman Fall limestone) in northwestern New York. The same beds have yielded late stages of endoceroids, the early stages of which are missing. Such specimens have been identified as *Endoceras proteiforme*, *E. angusticameratum* and *E. magniventrum*. Variation in proportions indicates clearly that this association contains several valid species of smooth endoceroids, probably all members of *Endoceras*. It is probable that their early stages are all similar, but vary somewhat in proportions. It is my belief that the apical portions of all of these species, whenever found, have been included under the name *Cameroceras trentonense*. A careful restudy of the endoceroids of the middle Trenton of New York is required to re-evaluate the species, and to connect young and adult portions. The writer had for some years accumulated material with this ultimate end in view, which is still inadequate and remains at the New York State Museum. Even should this study be completed satisfactorily, the status of *Cameroceras* will remain in doubt, for without Conrad's type, which is apparently irretrievably lost, it will not be possible to tell to which of the species of *Endoceras* it actually belongs. There is no doubt but that *Cameroceras trentonense* is the early stage of one of these species of endoceroids, but inasmuch as the species cannot be recognized, the generic name may be best relegated to the "genera dubia."

This is not as unfortunate as it might appear. The above survey shows that the generic name *Cameroceras* has been used loosely in the past, so loosely that it means nothing except that the shell to which it was applied was some sort of endoceroid. Its dissappearance from future literature will deprive us of little more than a catch-all for species which are inadequately known. The ressurrection of the name, and its attachment to a definite and recognized generic group within the endoceroids, would require a considerable upheaval in the present nomenclature. Almost certainly, *Endoceras* would have to be suppressed as a junior synonym of *Cameroceras*. This in itself is not bad, though the suppression of this widely employed name would have its unfortunate aspects. Greater confusion would, however, be caused by the suppression of the higher categories based upon *Endoceras*, the family Endoceratidae and the order Endoceratida.

Genus VAGINOCERAS Hyatt

Genotype: *Orthoceras multitubulatum* Hall.

Vaginoceras HYATT, 1883, Boston Soc. Nat. Hist., Proc., vol. 22, p. 266. ——, HYATT, 1900, Cephalopoda, in Zittel-Eastman Textb. Paleont., vol. 1, 1st. ed., p. 514. ——, RUEDEMANN, 1906, New York State Mus., Bull. 90, p. 412. ——, GRABAU & SHIMER, 1910, North American Index Fossils, vol. 2, p. 41.

Endoceras FOERSTE, 1924, Denison Univ. Bull., Sci. Lab., Jour., vol. 20, p. 208.

Vaginoceras TROEDSSON, 1926, Meddelelser om Grønland, bd. 71, p. 25. ——, KOBAYASHI, 1934, Tokyo Imp. Univ., Fac. Sci., Jour., sec. 2, vol. 3, 382, 387.

Endoceras MILLER & KUMMEL, 1944, Carnegie Mus., Annals, vol. 30, p. 21, 23.

The following description of *Vaginoceras* is based upon the general features of the type species, from the Black River limestone of the Watertown region of New York (see Pl. 34, figs. 1–2).

Shells are straight endoceroids, with transverse sutures, the cross section slightly depressed in section, but sometimes nearly circular, the vertical flattening being slight. Shell surface essentially smooth.

Siphuncle located close to the ventral wall, but usually narrowly separated from it, very slightly wider than high in cross section, but without flattening of the ventral side.

Siphuncle wall similar to that of *Endoceras*, with holochoanitic septal necks supplemented by connecting rings terminating in eyelets. The ring is thicker than in most species of *Endoceras*, less lobate in vertical section, and in general the septal necks and connecting rings seem to be more integrated in form and thickness into a seemingly simple siphuncle wall, the real differentiation of septal necks and connecting rings being often obscure enough to require study by thin section to make out the true structure. The rings commonly form a cushion between the siphuncle wall and the endosiphuncles, smoothing out the annular markings. Isolated endosiphuncles are therefore often smooth externally. While the smooth endosiphuncle is characteristic of *Vaginoceras*, this feature is probably not a good criterion separating the genus from *Endoceras*.

Thus far there are no significant features by which the genus can be distinguished from *Endoceras*. Such differences are found in the endosiphuncle. The endocones are not circular, but compressed in cross section, and cuneate, the ventral side being acutely subangular, the dorsal side more broadly rounded. Cross sections of the siphuncle show that the cones, and the compressed central tube in which they terminate, are connected with the outside of the endosiphuncle by two vertical blades (see Text-fig. 2K; Pl. 34, fig. 1–2).

How many species should be recognized in *Vaginoceras* is a difficult question. Typical encoceroid specimens are such small fragments of the whole that specific identification is sometimes uncomfortably close to being wishful thinking. In the opinion of the writer, the two species, *V. multitubulatum* and *V. longissimum*, of the Black River limestone can, from the present evidence, be two preservation phases of the same species. Material adequate for a proper evaluation of variations in proportions which might yield an indication of more than one species in this association is yet to be collected, assembled and studied.

It is more important, however, to note that *Vaginoceras* as thus defined is extremely characteristic of the faunas of Black River age and affinities. I have not found it in the Chazyan, nor in typical middle Trenton faunas. I have found it in the Black River (Chaumont limestones of New York), where it is dominant. The only other endoceroid genus which I have found there is *Cyclendoceras*. I have found indication of it in the underlying Lowville. It is the only endoceroid type I have seen in material from the Paquette rapids of the Ottawa River, an association which I regard as late Black River rather than early Trenton. The form which Troedsson (1926, p. 25. pl. 3, fig. 1–3) assigned to *Vaginoceras longissimum* is certainly a valid member of the genus *Vaginoceras*. It is probably a distinct species, as the cone terminates in the ventral part of the siphuncle rather than in the center. Its presence in the Platteville is suspected, but not as yet clearly demonstrated.

I have failed to find in the Black River limestone any well preserved specimens showing the initial part of the siphuncle which I could attribute to *Vaginoceras* with certainty. I have found, in fact, only one rather fragmentary specimen representing the early part of the siphuncle. This specimen showed that the apical end of the siphuncle was not swollen as in the genus *Nanno*, or *Suecoceras*, but tapered gently to the apex of the shell. If so, this will supply a further distinction between *Vaginoceras* and *Endoceras*. Whiteaves (1905) figured an apical end of a siphuncle of *Foerstellites* type from the Paquette Rapids, where *Vaginoceras* is common, but true *Endoceras* has not been found. This lends further support to the above conclusion.

In the abundant but extremely fragmentary endoceroids of the Cincinnatian I have

found no siphuncles typical of *Vaginoceras*. The Cincinnatian has, however, yielded some siphuncles in which the endocones are triangular in cross section (Text-fig. 2M). The material so far observed has been extremely poor and fragmentary; much of it was from old collections, and the exact horizon was unknown. An origin in the Eden or lowermost Covington is suspected. These forms may be a modified descendant of *Vaginoceras*, but should probably be made the basis of a separate genus when they are more adequately known.

There has been much confusion as to what constitutes the genus *Vaginoceras* Hyatt. Hyatt originally defined the genus as having long septal funnels (necks) which extend for more than the length of one camera. This definition was accepted by Ruedemann (1905) and Grabau and Shimer (1910). Foerste never employed the generic name, but regarded *Vaginoceras* as a synonym of *Endoceras*. Foerste (1924) considered the relatively long and numerous endocones the only feature separating *Vaginoceras* from *Endoceras*. He regarded this as insufficient basis for distinguishing the genera, and in subsequent works assigned species to *Endoceras* but did not use the name *Vaginoceras*. Troedsson (1926) states of *Vaginoceras:* "To this genus I have referred all siphuncle with numerous endocones; the endocones taper gradually downwards to a point, and their walls are not, as in *Cameroceras*, in contact with the walls of the siphuncle." He notes that Foerste did not consider the length of the septal neck as an additional distinguishing character, between *Endoceras* and *Vaginoceras*, because these two features, instead of being congruent, seem to be quite independent mutually.

Kobayashi in several papers referred a number of Asiatic species to *Vaginoceras*, but did not usually discuss the genus or supply a definition of it. It is interesting to note that for *V. grabaui* (Kobayashi, 1935, Japanese Jour. Geol. and Geog., vol. 5, p. 178–9) he figures long septal necks like those described by Hyatt (1884), later illustrated by him (1900) and accepted by Ruedemann (1906) for *Vaginoceras oppletum*. It is not evident whether the necks are long as in *Dideroceras* or whether their apices represent specializations or the ring as in *Vaginoceras oppletum* Ruedemann. Kobayashi (1934) defined *Vaginoceras* as "Conch circular to elliptical in cross section, siphuncle central to subventral; endosheaths numerous, and taper slowly." In contrast, *Endoceras* is regarded as having shorter endocones.

With this definition of *Vaginoceras* several genera have been proposed as differing from *Vaginoceras* in several features. This requires re-evaluation, inasmuch as Kobayashi's definition of the genus is not particularly consistent with the revised definition required by the restudy of the type species.

Miller and Kummel (1944) regarded *Vaginoceras* as a synonym of *Endoceras*. While the siphuncle walls do not show the differences which Hyatt (1884) used in separating the genera, the endosiphuncles are very different, and the genera therefore are regarded as valid and distinct.

So many specimens of *Vaginoceras* are extremely fragmentary that at the present time specific distinctions in the genus are only approximate. *V. oppletum* Ruedemann of the Chazyan is certainly not a true *Vaginoceras*. I have not changed the generic designation, other than placing it in quotation marks, because further study is needed to determine whether this species is best placed in *Endoceras*, or whether it belongs in a new genus. The problem is further complicated because generic names already proposed but incompletely defined must receive consideration.

The long necks with Hyatt attributed to *Vaginoceras* occur in a group of species typified by *Endoceras wahlenbergi* Foord, and the generic name *Dideroceras* Flower (1950) has been proposed for these species.

Genus PROENDOCERAS Flower, n. gen.

Genotype: *"Cameroceras" annuliferum* Flower, 1941, Paleontographica Americana, vol. 3, no. 12, p. 25, pl. 1, fig. 9–10.

Shell orthoconic, slightly depressed in cross section, sutures straight and transverse or nearly so, the shell resembling *Pachendoceras* in general aspect. Siphuncle tubular, ventral, septal necks very short in the young, with connecting rings relatively thin and apparently homogeneous in structure. Later segments show elongation of the necks and differentiation of the ring into two parts (Flower, 1947, p. 163, fig. 1C) the

inner part being thin adorally, thick apically, and suggesting a transition from the layered structure of *Proterocameroceras* to the eyelet developed in more specialized endoceroids. Apically the siphuncle tapers gently to a small diameter and then terminates in a blunt tip. The apical part of the siphuncle is very slightly curved, faintly convex on the ventral side. Camerae enclosed the siphuncle laterally and dorsally at least to the tip of the shell.

Discussion.—This genus is erected for the most generalized endoceroids known in the Canadian. It includes shells of the gross aspect of *Pachendoceras*, but which possess endocones. Cones are simple, circular in cross section as far as known, and terminate in a central tube which, in the genotype, is faintly annular. No blades have been observed in the genotype.

The writer had been previously of the opinion that the genus *Cyptendoceras* might be redefined to include the species of generalized form, section and suture pattern for which *Proendoceras* is now erected. Subsequent study and consultation resulted in the conclusion that it was wiser to leave *Cyptendoceras* as originally defined and to create a new generic group for the more generalized forms. Both *Cyptendoceras* and *Cyptendocerina* possess ventral lobes of the sutures absent in *Proendoceras*. The isolated siphuncles of *Manitouoceras* are superficially similar, though they represent a greatly magnified edition of the early stage of *Proendoceras*.

If *Pachendoceras newportense* Ulrich, Foerste, Miller and Unklesbay of the Longview limestone of Virginia, and *Pachendoceras sayi* (Billings) of the Hastings Creek formation prove to be endoceroids, as seems highly likely, they will probably fall within the limits of *Proendoceras*. *Paraendoceras* differs in the more rapid expansion of the shell and the smaller diameter of the siphuncle. *Endoceras? wappingerense* Ulrich, Foerste, Miller and Unklesbay is a *Proendoceras*. *Endoceras? champlainense* will never be adequately known from topotype material, but occurs in the northward extension of the same fauna which yields *Proendoceras annuliferum*. It is quite certainly the same genus, and it is not possible to prove that the two are distinct species. *E. champlainense* is so poorly preserved that it is impossible to prove much of anything about it, and I hazard this opinion only because of apparent continuity of the faunas of the *Lecanospira* beds of the Lake Champlain region.

The known species occur in the *Lecanospira* beds of eastern North America, of approximately Roubidoux age.

Genus HUDSONOCERAS Flower, n. gen.

Genotype: *Hudsonoceras aristos* Flower, n. sp.

This genus is externally an extremely generalized endoceroid, straight and slender, with transverse sutures, a siphuncle which is in contact with the ventral wall of the shell. Present cross section of the shell slightly compressed, a condition which may only be the result of slight flattening of a specimen which was found resting on one lateral surface. The siphuncle wall is composed of septal necks which are very thin, but extend for the length of one and one-half segments of the siphuncle. Where the neck penetrates the next adapical segment, it is separated by a thin connecting ring from the base of the next adapical septal neck. Beyond its tip, this connecting ring becomes thicker and darker in color, showing the same dark color and amorphous structure which characterizes the eyelet in some other endoceroids, notably "*Vaginoceras*" *oppletum* Ruedemann. The anterior end of each segment of the siphuncle is faintly concave, the adapical end convex. The change in outline is located at the point of the termination of the inner septal neck.

The endosiphuncle shows in cross section two distinct regions, a ventral mass which shows a convex inner surface, so that the speiss, the internal mold of the endosiphocone, is concave ventrally, and a typical thinner dorsal region in which the endocones conform to the cross section of the siphuncle. The two areas are sharply separated by dark lines, curved, the convexity directed outward. At the regions where the endocones fill the siphuncle completely, these two lines join to form an arc, at the apex of which is an extremely tiny and inconspicious tube. Sections through the apical part of the siphuncle may show, though with variable clarity, two dorso-

lateral pair of endosiphoblades, and one blade on the midventral side. Vertical sections through the siphuncle exhibit rather widely spaced perfectly straight transverse lines running from the siphuncle wall to the center, structures unlike anything previously observed in endoceroids. Though roughly agreeing in spacing with the segmentation of the exterior of the siphuncle, they apparently have little if anything to do with the siphuncle wall; they are perfectly transverse in vertical longitudinal section, while the annular markings of the exterior of the siphuncle slope apicad from venter to dorsum, as is true of practically all endoceroids.

Discussion.—The general pattern of the siphuncle of this genus is closely similar to that of *Coreanoceras*, known primarily from the Wolungian (upper Canadian) of Manchuria. There are, however, a number of important differences. The septal necks of *Coreanoceras* are reported as being very short; those of the present genus are surpassed in length only by those of *Dideroceras* of the *Orthoceras* limestone, and *Chisiloceras* from equivalent strata of southeastern Asia. Neither of these genera is at all comparable in the features of the endosiphuncle; their endocones are extremely simple in cross section. Kobayashi has regarded *Coreanoceras* as a piloceroid. While the distinction between the slender endoceroids and the rapidly expanding piloceroids is one in which transitions may reasonably be expected, in the opinion of the writer *Coreanoceras* is comparable in proportion with the siphuncles of many slender endoceroids. Larger species of essentially slender endoceroids of the Proterocameroceratidae, have siphuncles the early stages of which exhibit essentially the proportions of *Coreanoceras*.

The siphuncle of *Hudsonoceras* shows regular lamellae of growth in the ventral mass, and lacks any structure which could be interpreted as a secondary alveolus or endocone which Kobayashi attributes to *Coreanoceras*. Nothing similar to the regular widely spaced bands crossing the siphuncle has been noted in *Coreanoceras*, or any other endoceroid genus for that matter. The numerous faint blades indicated in some of the sections of *Hudsonoceras* are paralleled only by those of a Canadian genus to be described later, which differs markedly in other features of the endocone and is probably not closely related.

The shell surface of *Hudsonoceras* was apparently virtually smooth. The condition of the apex of the siphuncle and of the shell is unknown.

The position of *Hudsonoceras* in the endoceroids poses an interesting problem. Its endosiphuncle indicates that it is a logical descendant of *Coreanoceras*, in which there is a remarkable elongation of the septal necks. On the basis of the siphuncle wall, one could postulate instead that this genus is a relative of *Dideroceras* in which the endosiphuncle parallels that of *Coreanoceras*.

The relationship to *Coreanoceras* seems the more probable of these two possibilities. The tendency toward elongation of the septal necks in endoceroids is evident; it may well have continued to extremes in more than one line of descent. The endosiphuncles of *Dideroceras* and *Chisiloceras* are extremely simple; the cones are circular, the tube central, blades are not clearly differentiated. The morphological gap separating *Hudsonoceras* from *Dideroceras* seems much greater than that separating it from *Coreanoceras*.

HUDSONOCERAS ARISTOS Flower, n. sp.
Pl. 32, figs. 1–4; Pl. 33, figs. 1–13;
Text-fig. 3

This species is based upon a single endoceroid of relatively large size. The specimen, when found, presented a poor natural section, which was very nearly vertical, on one surface. The other surface was removed from the matrix and is shown on Pl. 32, fig. 1. This specimen, 38 cm. in length, consists of an apical interval of 23 cm. of exposed siphuncle, followed by 68 cm. of shell. The exposed portion of the siphuncle is essentially circular in section, and expands from 21 to 23 mm. in diameter. The shell increases in height from 55 to 125 mm. in 680 mm. The main part of the shell is septate. In the 555 mm. of the phragmocone the spacing of the septa increases only gradually; apically eight camerae occupy a length of 10 cm., adorally six occur in an equal length. In the length of the phragmocone the siphuncle expands from 23 to 55 mm. in diameter. The adoral 16 cm. of the

shell represent the basal part of a living chamber of unknown length when complete. The cross section of the shell appears to have been slightly higher than wide. As the shell lay on a lateral surface, this effect may be the result of slight flattening, rather than a natural condition. Of the 555 mm. of the phragmocone, the adoral 330 mm. encloses a siphuncle free from any endocones. From this point the speiss extends from 1 in Pl. 32, fig. 1, apicad 30 cm. to 4 in the same figure. Vexingly, portions of this species failing to show the endosiphuncle or retaining the siphuncle wall clearly, could not be identified with any real certainty.

The siphuncle is essentially circular in cross section. Each septal neck extends for the length of one and one half segments. The apical portion of the neck which invaginates into the next, is separated from it by an extremely narrow connecting ring, relatively light in color in opaque section. Beyond the tip of the neck, this connecting ring becomes dark in color, amorphous in structure, and resembling the eyelets of *"Vaginoceras" appletum* Ruedemann (see Flower, 1941), and continues on the inner surface of the next septal neck to its very tip (Text-fig. 3a, Pl. 32, figs. 3–4). Similar siphuncle walls have thus far been observed only in *Dideroceras* and *Chisiloceras*. A section taken farther apicad, shows apparent septal necks, with connecting rings along their inner surfaces, which are only half a segment in length (Text-fig. 3B). This is regarded as the result of abrasion of the siphuncle prior to burial. The anterior end of each segment of the siphuncle is faintly concave. Curvature is reversed in the apical part, and the reversal occurs at the point of termination of the invaginated septal neck. It is believed that the outer part of the siphuncle wall is here abraded, and that only the inner part, being in part protected by the concave outline of this part of the segment, has been preserved. (See Pl. 33, fig. 13).

The endosiphuncle is made up of numerous long extremely thin endocones, their surfaces represented by closely spaced growth lines seen in numerous transverse sections. In general, the endocones consist of two very distinct regions, a large ventral mass, the inner surface of which is convex, and thin more typical dorsal endocones, the inner surfaces of which are concave and conform to the cross section of the siphuncle. The two areas are set apart by a pair of

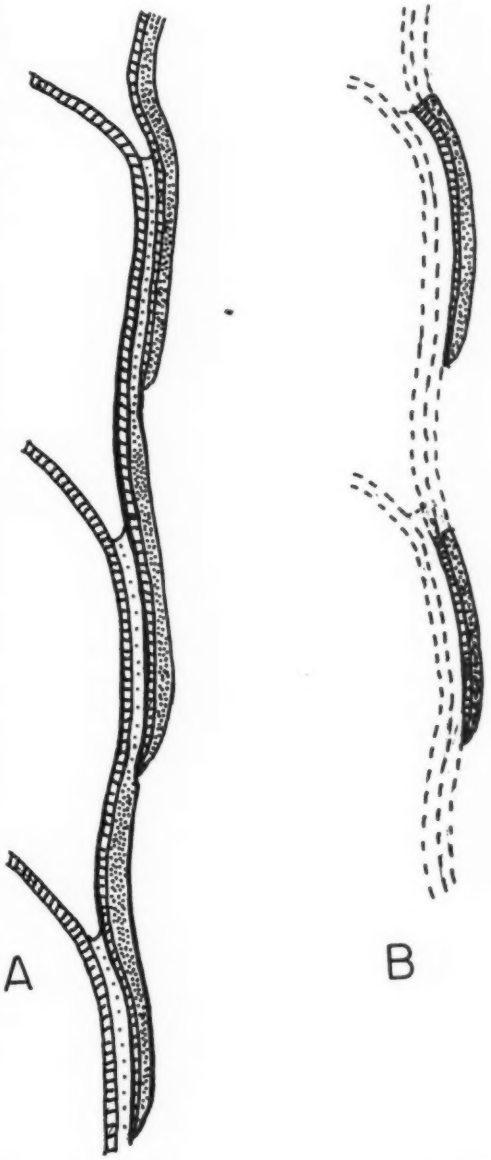

FIG. 3—Siphuncle wall of *Hudsonoceras aristos*. A. Complete siphuncle wall, with thickness of rings and necks slightly exaggerated. Based upon Pl. 1, fig. 4. B. Interpretation of condition found in adapical part showing neck and ring as seen, with missing parts restored.

curved dark lines, here referred to as primary endosiphoblades. Sections taken at or apicad of the tip of the endosiphocone, show these two blades uniting to form an arc, at the apex of which lies the endosiphotube, which is often tiny and extremely inconspicuous. Sections from the adoral part of the siphuncle show only normal lamellae of growth of the endocones. Sections in the apical part, however, may show fainter radial structures, a series of structures probably more closely related to the blades of other endoceroids than the primary blades which are more conspicuous and constant features in *Hudosnoceras*. There can be seen two pairs of dorsolateral blades, a midventral blade, and traces of a fainter median dorsal blade. Longitudinal sections through the siphuncle (Pl. 32, fig. 3, Pl. 33, fig. 13) show, within the endocone material, darker transverse lines, passing horizontally from the center of the siphuncle to the wall on either side. These structures are regularly repeated. They fail to show any evidence of tubular structure, and cannot be regarded as vascular structures connecting the central tube with the camerae. Not only is there no trace of tubular structure, but there is quite obviously no connection possible through the siphuncle wall at their tips. Further, it may be noted that these structures are transverse and perfectly normal to the axis of the siphuncle, as seen in vertical section, while in contrast the wall structure of the siphuncle is markedly askew, all septal markings sloping forward strongly from the dorsal to the ventral side, as is true of most endoceroids with ventral siphuncles.

The endosiphuncle was studied from a series of cross sections shown on Pl. 33. Before discussing them in detail, a word must be said concerning the preservation of the specimen. This shell was found with the upper (dorsolateral) region eroded and parallel to the surface of the surrounding rock. It would naturally be supposed that this was completely the result of normal recent erosion. However, the entire specimen is pitted with small round cavities which extend for varying distances down from the upper surface. These cavities penetrate the calcite of the endosiphuncle, but also penetrate the matrix. They are apparently the work of some boring organism, which acted upon the upper surface of the shell as it lay in the sediments. Furthermore, their abundance on the upper surface indicates quite strongly that they acted upon a shell which had not only been buried in this position, and the matrix around it quite well consolidated, but that in all probability the upper surface was eroded to or close to the plane of the present weathered surface, that the boring organism acted upon this weathered surface, all of this prior to the deposition of the next layer of limestone which covered the one enclosing the cephalopod shell. Similar flattening of the upper surfaces of internal molds of large cephalopods has been noted elsewhere. The matter is of importance at this point, because the numerous irregular cavities penetrate far enough into the shell to present anomalies in the transverse sections; in attempting to interpret the original structure of the shell, they must be recognized for what they are, and discounted insofar as any original shell structures are concerned.

The normal appearance of a cross section is shown in Pl. 32, fig. 2. This is a composite of photographs of the mirror images on two sides of a section taken at the point 3 on the complete specimen shown in Pl. 32, fig. 1. The calcite is broken in the lower left, obscuring the primary blade in that region; the dark spot just to the right of the top of the figure represents one of the cavities produced by an unknown boring organism.

Pl. 33 is largely devoted to illustration of the sections of the endosiphuncle. Pl. 33, fig. 1 is taken at point 2 on Pl. 32, fig. 1, and is slightly more than twice natural size. This lies at the base of the longitudinal section shown on Pl. 32, fig. 3. A boring interrupts the dorsal endocones just to the left of the tip of the figure. The ventral mass, the one lateral primary blade, and lamellae of growth in the entire endosiphuncle can be seen. The next two sections, Pl. 33, figs. 2 and 3, are shown natural size. Fig. 2 lies 38 mm. apicad of fig. 1, at position 3 on Pl. 32, fig. 1. Its mirror image is separated from it by a lost interval of about 2.5 mm. As these two sections together form the basis of Pl. 32, fig. 2, they are not shown here in enlargment, though it is necessary to show some slight differences which they present. Fig. 2 shows some borings in the

lower right within the ventral mass. The mass itself shows lamellae of growth, and lacks the short black vertical line at the bottom shown by its mirror image on fig. 3. It should be noted that the dorso-lateral region of figs. 1, 2 and 3 shows a faint band which might be construed as the homologue of a dorso-lateral blade, not seen in the succeeding sections (figs. 4–5) but which reappears in some later ones.

Figs. 4 and 5, lie 54 mm. farther apicad, and are again separated by a lost interval of about 2.5 mm. They are again complicated by borings, at the bottom of fig. 4 and on the upper left of fig. 5. Lamellae of growth are seen in the cones, the endosiphocone is by now closer to its tip and greatly reduced in size, the primary blades are well developed, but no accessory blades are evident.

The next section, Pl. 33, fig. 6, lies at least 60 mm. farther apicad; the exact distance being uncertain, because of a break in the siphuncle and a crumbling of some of the material. Fig. 6 shows the two primary blades forming a complete arc, with a small lenticular body at its apex which apparently represents the very tip of the endosiphocone. In the mirror image of this section (Pl. 33, fig. 7) this body is not visible, and the tube into which the cone generally terminates is so small that it cannot be seen as a widening or even a darkening of the primary blades. In both sections lamellae of growth of the cones can be seen. There is further a trace of a dorso-lateral blade, and possibly a trace of a median dorsal blade, though it is visible only near the center of the siphuncle here.

The next section, Pl. 33, fig. 8, taken 38 mm. farther apicad, shows, dorsad of the line of the primary blades, a dark band outlining an oval area. From this body two dark bands extend obliquely to the dorsolateral wall of the siphuncle. From its base a median blade extends to the ventral wall. Three borings are visible on the right side of this section.

So remarkable is the appearance of this section, that a vertical section was taken between the sections illustrated on Pl. 33, figs. 7 and 8 to ascertain the nature of the oval body. This section, Pl. 33, fig. 13, shows that there is here an endocone surface of unusual clarity. Within the center of it can be seen a median dark line marking the position of the primary blades and the endosiphotube. In the section of fig. 8 the dorsal part of the endocone is clearly seen; its ventral outline cannot, however, be made out. There results the effect of a lenticular body dorsad of the blade, which would be a completely unexpected and bizarre structure to find here. The same section shows the incomplete preservation of spetal necks and connecting rings already noted, and intepreted in Text-fig. 3b. It also shows the transverse dark lines crossing the siphuncle, which have been discussed above. Pl. 33, fig. 9, is the mirror image of the section shown on fig. 8. It exhibits the same central structure, two dorsolateral blades, but there is no trace of the ventral blade. The curved primary blades are, as usual, clear.

The next section (Pl. 33, fig. 10), and its mirror image (fig. 11), shows a lenticular central canal, primary blades, one dorsolateral assessory blade, and a fainter one of the second dorso-lateral pair. A ventral blade (?) shown irregularly in fig. 10 and more regularly in fig. 11, is present. The upper left side of fig. 11 is again complicated by borings. The last section, fig. 12, shows a curved flat tube, and both the primary and secondary blades are extremely faintly differentiated. It should be noted that the specimen terminates 4 mm. beyond this section. The remaining apical part of the siphuncle has not been found.

Discussion.—This large endoceroid, externally so generalized in aspect, is one of many forms which have been customarily identified as *Cameroceras tenuiseptum* (Hall). As pointed out, in the discussion of the genus, the interior of the siphuncle agrees more closely with that of *Coreanoceras* than with that of any other described genus, but the repeated transverse lines seen in longitudinal sections, the secondary blades, the absence of a ventral alveolus (dubious as doubtfully demonstrated in *Coreanoceras*) indicate significant differences. More profound differences are found in the siphuncle wall, and in the evident fact that this is a large rather than a tiny endoceroid. For these reasons, this species is set apart in a different genus.

In numerous sections of other Chazyan

endoceroids nothing similar to the present species has been found. The type is in the collection of the writer.

Occurrence.—From the Chazyan limestone, from beds attributed to the upper (Valcour) division of the Chazyan, from the bay just north of Cystid Point on the southeast corner of Valcour Island, Lake Champlain.

Family ALLOTRIOCERATIDAE Flower, n. fam.

Endoceroids, thus far known only from siphuncles. Condition of siphuncle wall not yet ascertained. The family is characterized primarily by complex endocones and multiple endosiphotubes present in some stage of growth. The modification of the cones is due to the presence of structures which are deposited prior to the endocones. In *Allotrioceras* they consist of a lining from which there extends a forked process dividing the cavity of the siphuncle into two lateral areas, in each of which endocones later appear. In *Mirabiloceras* the lining is suppressed, but instead there is a central pillar, and the cones are continuous around its circumference.

Relationships.—The two genera for which this family is erected are seemingly so different from other endoceroids, and even from each other, that any connection is necessarily inferential. Plainly, *Allotrioceras* owes its distinctive features to the appearance of an endosipholining, from which extends a septum nearly dividing the siphuncle into two lateral areas. Further, its tip is forked. This is a completely new feature in endoceroids. However, one may postulate that any endoceroid in which such features develop, would of necessity have the endocones, secreted later, divided into two lateral areas. The manner in which this structure could have originated from a more generalized endoceroid is shown in Text-fig. 4. It has been noted that in *Meniscoceras* a dark line, interpreted as a blade, is sometimes apparent extending from the dorsal wall of the siphuncle toward its center. The endocones are semicircular in cross section, the angles marked by two prominent lateral dark blades (Text-fig. 4A).

Figure 4B is a hypothetical stage showing the natural modifications which would be expected if the development of cones is preceded by a lining of the siphuncle which also outlines the median blade. The cones would be nearly divided into two parts, and eventually each part would tend to terminate in its own tube. This is only a transitional stage to *Allotrioceras bifurcatum*,

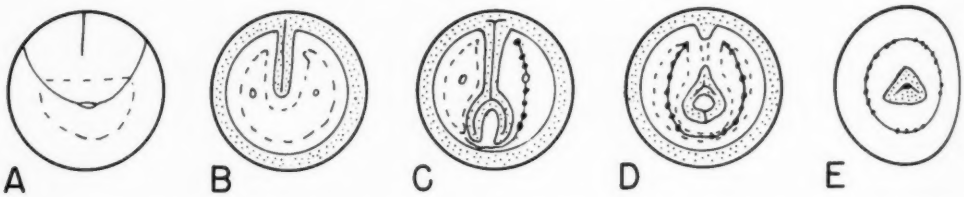

FIG. 4—Hypothetical relationship of *Allotrioceras* and *Mirabiloceras* with each other and with the more generalized *Meniscoceras*, shown by cross sections of endosiphuncles. A. *Meniscoceras coronense* showing two lateral blades and middorsal blade. Cross section of a single endocone surface is indicated in a broken line. B. Hypothetical. Endosipholining (stippled) forms within ectosiphuncle and outlines the middorsal blade, which now becomes a septum, in accordance with which the section of the endocones is further modified, the tube dividing into two lateral tubes. C. *Allotrioceras bifurcatum*. Septum more strongly developed, its tip bifurcated. Cones are now divided completely into two lateral entities. Adorally, as on the left, there is a single tube in each lateral area. Apically, as shown on the right, there are multiple tubes connected by a dark band. Cones disappear here, and consequently are not indicated. D. Hypothetical stage leading to *Mirabiloceras*. Lining remains, but the middle of the septum is suppressed. The two prongs of the fork have joined, and are nearly central in position, permitting the lateral cones to join around its tip, though they are still discontinuous over the region of the base of the septum. E. *Mirabiloceras multitubulatum*. The lining is suppressed. The two prongs at the tip of the septum have fused surrounding a small triangular space. The endocones form a complete circle around the pillar, terminating in a dark band joining the numerous tubes. Tubes seem to be concentrated in three regions opposite the faces of the triangular pillar.

Text-fig. 4C. The lining is present as before. The septum is now much longer, and its tip is forked. The endocones are now well separated into two lateral units. In the adoral part of the shell, as indicated on the left, the individual cones are distinct, and terminate in a central tube on each side. The early stages show a more advanced condition, which must follow the condition found in the later growth stages in evolutionary development. The boundaries between the individual cones dissappear, and a dark band lying in such a position as to connect the acute angles of the lateral endocones, connects a series of several tubes.

Text-fig. 4D is a hypothetical stage, in which the base of the septum is suppressed, the forked tip lies now in a central position, the prongs closed. The lateral endocones have joined around the tip of the former septum, but are not yet continuous over the base of the septum. Multiple tubes are connected by a dark band.

Text-fig. 4E is the condition actually observed in *Mirabiloceras multitubulatum*. The lining as well as the base of the septum is now suppressed. The forked tip has its prongs completely fused. The endocones are continuous around the circumference of the central pillar. Rapid and continuous growth is suggested by the absence of clear surfaces of individual endocones, a feature already presaged by the coenogenetic features of the early stage of *Allotrioceras*.

It should be noted that in neither *Mirabiloceras* nor *Allotrioceras* is there definite evidence as to which side of the siphuncle is dorsal and which is ventral. Comparison with *Meniscoceras* suggests that the septum may originate from the dorsal wall. However, a reversed orientation could be postulated. Traces of median ventral blades have been found in *Manchuroceras* and *Coreanoceras* although Kobayashi has regarded those regions as marked, not by any positive structure which is likely to be prolonged into the siphuncle but rather as a cavity, an alveolus, or a small secondary endocone cavity. Although I regard the evidence of the alveolus as somewhat doubtful, until the possibility can be explored more thoroughly, its proposal surrounds with vexations any attempt to postulate the origin of the septum of the genus *Allotrioceras* from the short vertical dark line observed on the ventral side of either of these genera.

Genus ALLOTRIOCERAS Flower, n. gen.

Genotype: *Allotrioceras bifurcatum* Flower, n. sp.

This genus is as yet known only from the endosiphuncle. Externally, it is slender and nondescript, the annular markings of the septa not clearly displayed on the one known specimen of the single known species. At the adoral end of the siphuncle there is seen only a calcareous lining, from which a median septum extends from one wall nearly to the next, its tip bifurcated. Calcareous deposits eventually fill in the area between the two forks of the septum, but the filling is not obviously composed of endocones. A series of endocones develops in each of the two major lateral areas, the tips terminating in a pair of prominent endosiphotubes.

In the adapical part of the siphuncle the outlines of the cones are no longer clear. Instead, there is developed a dark band, comparable to the endosiphoblades of other endoceroids in appearance, which passes through the acute angles of the lateral endocones, as well as through the central endosiphotubes. The dark band continues around the fork of the septum, here broad, and somewhat askew, to form a continuous arc. On closer examination this dark band is found to have incorporated in it, not only the two lateral endosiphotubes which would reasonably be expected, but a series of numerous small longitudinal tubes concentrated in each of the two main lateral areas.

Discussion.—This genus is absolutely unique, both in the adoral part, with a lining, bifurcated septum, and endocones located in the two lateral cavities, and in the apical part, where multiple endosiphotubes are formed in each of the lateral areas. It should further be noted that the multiple tubes, which are confined to the early portion, are not structures which could conceivably have been developed there by secondary alteration; rather they must represent a coenogenetic feature developed only in the young stage of this form. Their function is unknown; indeed, the function of the single endosiphotube in most

endoceroids is a structure for which no convincing function has yet been suggested. The multiple tubes obviously represent a specialized condition, and one previously unknown in endoceroids.

ALLOTRIOCERAS BIFURCATUM Flower, n. sp.
Pl. 34, figs. 3–19; Text-fig. 6A–H

This species is based upon a single endosiphuncle 160 mm. in length, slightly depressed in cross section, the two sides equally flattened. There is no real clue as to which side is dorsal and which is ventral. The specimen is oriented in the following descriptions and illustrations in the position in which it lay in the rock, with the septum arising from the upper, apparently dorsal, margin of the siphuncle, but it should be pointed out that any orientation is necessarily arbitrary, and must remain so until more complete specimens have been found. The siphuncle is slender throughout, increasing in width from 8 mm. at the apical end to 17 mm. at the adoral end.

A cross section close to the anterior end of the siphuncle shows a lining of white calcite (Pl. 34, fig. 4,) containing traces of concentric growth bands. From this, at the top of the figure, a septum descends, broad basally, narrow centrally, wider beyond the middle, the tip divided into two prongs. Pl. 34, fig. 3 shows the same section in the lower half, but the upper half is a transverse longitudinal section showing the adoral limit of the endosipholining, and also of the septum in the plane of the section. It is believed, from the thinning of the septum in the middle, that the anterior end of the septum curves down (apicad) from its point of attachment, and rises at its forked tip, which extends slightly farther forward than does the endosipholining, as indicated in Text-fig. 6A.

The opposite surface from the same cut, in which about 2.5 mm. of material was lost (Pl. 34, fig. 5), shows the lining somewhat thicker, the septum thicker, still markedly thickened at its base and constricted at mid-length, the two forks of the tip nearly opposed. A median dark line can be seen in the basal part of the septum, which connects with a dark band which runs around the circumference, dividing the lining into two regions. Within the lining is a very thin layer of white calcite in the two lateral areas, representing the extreme adoral part of the adoral endocones.

The next section, 7.mm. farther apicad, Pl. 34, fig. 6, shows the prongs of the fork of the septum more widely separated; the area between is filled with calcite. The two lateral areas are about half filled in with endocones, the dark boundaries of which are clearly indicated. Pl. 34, fig. 7, is the mirror image of this section, again with a loss of about 2.5 mm. of material, and showing the lateral endocones now markedly closer to their apices.

The next section, Pl. 34, fig. 8., was taken 30 mm. farther apicad, to avoid a natural break in the middle part of the specimen. Here the two prongs of the fork are widely separated, very slightly askew from the plane of symmetry, the lateral areas are filled in solid with endocones, though the endosiphotubes are not evident, possibly from recrystallization. The outer endocone surfaces are indicated clearly by dark if somewhat faint concentric bands, largely semicircular in cross section.

In the succeeding interval, the siphuncle was cut horizontally, as shown in Pl. 34, fig. 9. The lower surface of this part of the specimen is shown in Pl. 34, fig. 11; here, in the two lateral regions, the endocones are very clearly indicated. They are separated by a median dark band, the axis of the vertical septum, but the walls of the septum are not clearly displayed. The mirror image of this section, Pl. 34, fig. 10, 2.5 mm. ventrad of the other, shows the endocones somewhat less clearly, but at the anterior end of the specimen, the width of the median septum is clearly indicated where its dark axis is crossed by several dark transverse bands. At this region another horizontal section was taken at the level of the forks of the septum, but is not figured. The lateral areas are occupied by endocones, which are not too well preserved. The area bounded by the two prongs of the fork is represented only by grey calcite; and fails to show endocones or any other definite structure.

The two longitudinal sections indicate a faint annular condition of the exterior of the siphuncle. The annuli are distant, indicating that the camerae were unusually widely

spaced in proportion to the diameter of the siphuncle.

The next cross section, Pl. 34, fig. 12, lies 38 mm. apicad of that shown in fig. 8. Here the aspect has changed markedly. The black median line of the septum is clear; its walls are obscure. At its base, two dark bands extend laterally for a short distance into the endosipholining, but cannot be traced far. On the lower side, the inner surface of the lining in indicated.

The fork of the septum has two widely separated branches, and is askew in relation to the rest of the section. The two lateral areas fail to show the section of the endocones clearly; instead, there is a prominent dark band which seems to connect the angular corners of the cones and the central canals. These bands on the two sides connect beneath the fork of the septum. Further, on one side, the left of this figure, the dark band is clearly broken up into several separate elements. The mirror image of this cut, fig. 13, shows much the same phenomena. The two sections together indicate that the broken part of the dark band represents cross sections of a series of small tubes which run longitudinally the length of the siphuncle in this region.

The next section (Pl. 34, fig. 14), taken 15 mm. farther apicad, shows the band on the right better developed than in the preceding section. That on the left is similar to that of the preceding sections. On both sides now the dark line is broken into discrete tubes, though those on the left are better developed than those on the right. The area enclosed by the fork is large, round, askew, and filled in with calcite which has evidently recrystallized. The sections in figs. 14 and 15, again mirror images, show a dark outer area; from the upper part, in fig. 15, are seen two short dark lines extending down and outlining part of the median septum, a feature found in no other sections.

In the next section, Pl. 34, fig. 16, the dark line connecting the tubes is prominent; on one side it terminates in a peculiar triangular area, not as yet fully explained, but evidently characteristic. The median septum is present, but shown only by relatively faint color contrast. The longitudinal section, Pl. 34, fig. 18, lies between Pl. 34, fig. 16, the mirror image of 15, and Pl. 34, fig. 19. It is noteworthy that this longitudinal section shows longitudinal elements, but the short endocones of the anterior end (Pl. 34, fig. 10–11), are no longer in evidence. It is as though this part of the siphuncle were filled in rapidly, leaving free only the longitudinal tubular elements connected by the dark line resembling an endosiphoblade. The anterior end of this piece is shown in fig. 17; the adapical end in fig. 19. Apicad of fig. 19, the specimen terminates. As the siphuncle here is only 8 mm. across, and expands gradually from that point orad as far as it is known, it seems very unlikely that there is any apical swelling of the *Nanno* or *Suecoceras* persuasion.

Discussion.—No trace of the shell wall, septa or siphuncle wall can be found. The faint annulations on the siphuncle suggest relatively distant septa. The features of the endosiphuncle are so remarkable that there is no other species with which this one can be confused.

Externally, annulations on the siphuncle are so obscure that their direction of slope, one of the best criteria of orientation, cannot be determined. As a consequence, it is not demonstrable whether the septum springs from the dorsal or ventral wall of the siphuncle.

The type and only known specimen I collected from the middle Chazyan on my first visit to the Champlain valley in 1934; so nondescript was it externally, that it was not until sixteen years later that it was sectioned and its truly remarkable structure was consequently seen. Moral: do not discard nondesdript endoceroid siphuncles. Either section them or send them to me.

The structure of this species is shown somewhat more clearly in Text-figure 6 A–H. Figure 6A represents the adoral portion. The septum is complete only in the adoral end; lower down, all hard parts are cut away to the middle, so that half of the lateral endocones can be seen. At the base, the remaining half of the cross section is restored. Figure 6B shows the tubes present in the adapical portion of the siphuncle; adorally their relation to the endocone pattern is indicated; adapically only the dark line, seemingly an endosiphoblade, is seen. The positions of the cross sections C through

G are indicated by corresponding small letter on figs. 6A and B. The numbers on fig. A represent the shell elements in the order in which they are formed, 1, the siphuncle wall, 2, the lining and its septum, 3, the adoral end of the last endocones, 4, termination of the cones, and beginning of the tubes. As cross sections are traced apicad, the disappearance of the outlines of the cones in cross section and the dominance of the tubes and the dark band connecting them, appears to be relatively gradual. Text-fig. 6H shows the hypothetical relationship of the position of the tubes with the angles of the endocones in cross section.

Holotype.—Collection of the writer.

Occurrence.—Middle Chazyan limestone, from the *Maclurites* beds exposed west of Chazy, New York, in the type section of Brainerd and Seely.

Genus MIRABILOCERAS Flower, n. gen.

Genotype: *Mirabiloceras multitubulatum* Flower, n. sp.

This genus is erected for the unique species described below which is known only from a portion of a siphuncle showing the anterior end of the endosiphuncle. The features of the shell are unknown; presumably the shell was slender and of endoceroid aspect. The apical portion of the siphuncle shows some traces of the ectosiphuncle. It is evident that the septa were unusually closely spaced. The structure of the siphuncle wall cannot be made out clearly. Discrete dark patches resemble the structure found in the early portion of *Hudsonoceras* (Text-fig. 3), but are open to other interpretations. There is, however, adequate evidence that the singular structure is an endosiphuncle clearly enclosed in a siphuncle wall of septal necks and connecting rings.

The general organization of the siphuncle is shown in Plate 35 and in the accompanying Text-figure 5. Before endocones were secreted, there grew forward in the siphuncle a central pillar, which is roughly the shape of an isosceles triangle in cross section. At its anterior end it is hollow, the cavity being triangular; later this cavity became filled in, leaving only a tiny central tube from which two lines can be seen extending some distance toward the two basal angles of the triangle. Forming a complete circle around the central pillar, lie the endocones. Their inner limb extends far forward, nearly reaching the apex of the pillar; their outer limb is relatively short. The termination of the tip of the cone is nearly if not exactly a circle lying in a plane

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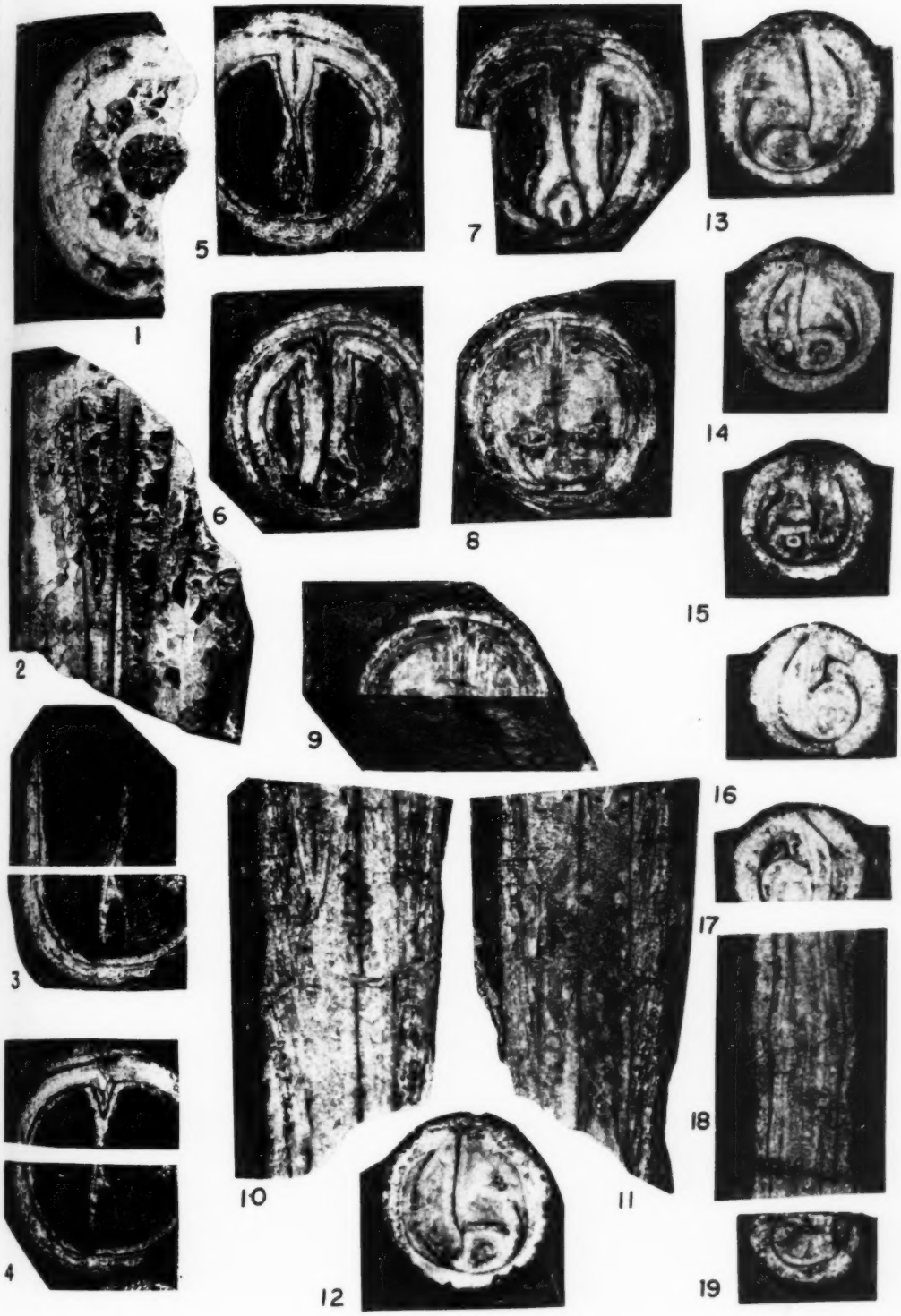
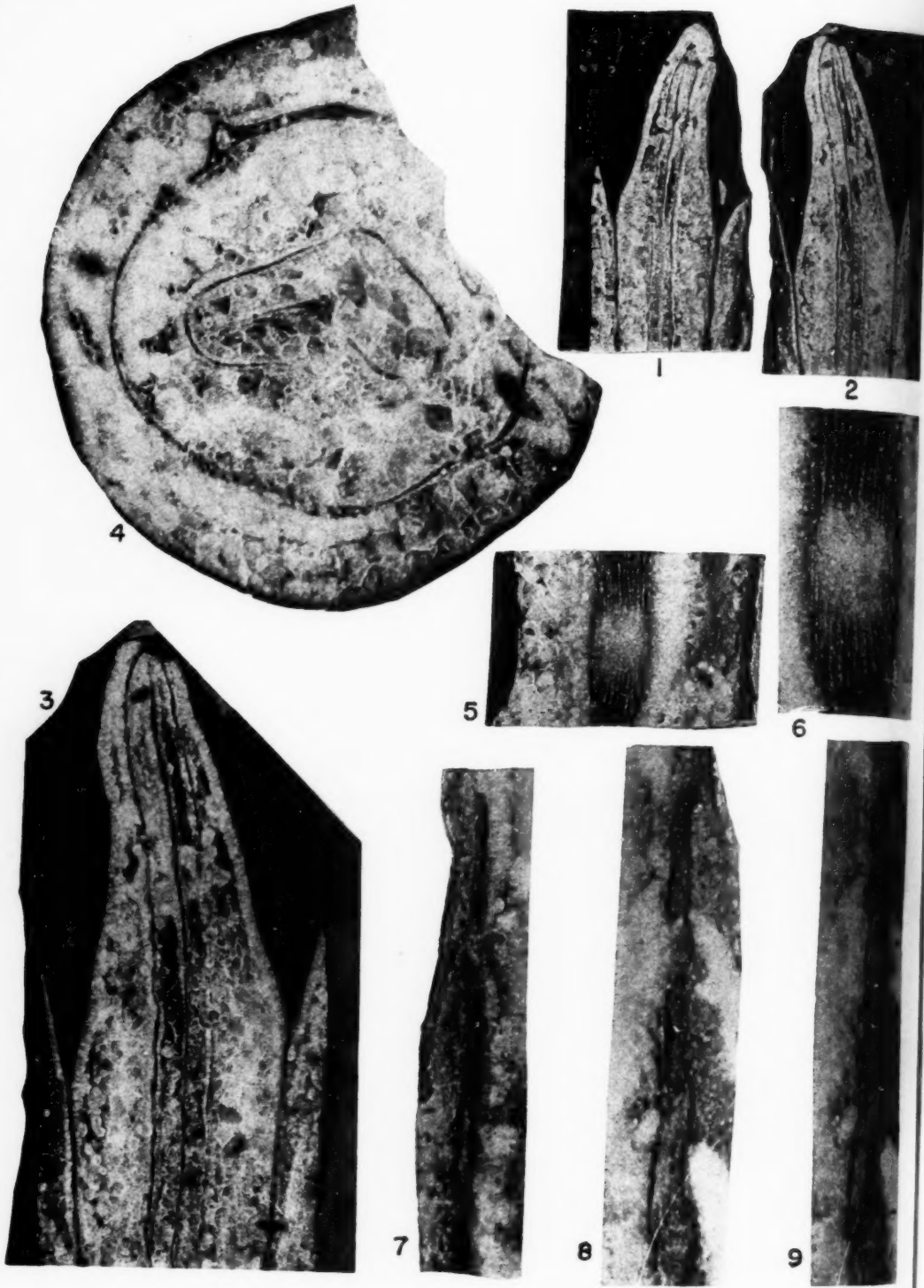
EXPLANATION OF PLATE 34

FIGS. *1–2*—*Vaginoceras multitubulatum* Hall. *1*, Cross section near base of speiss, with the broad dorsal end to the left, ×1.8. *2*, Longitudinal section showing cones and, in the lower half, the section cutting the tube, ×1.5. (p. 349)

3–19—*Allotrioceras bifurcatum* Flower, n. sp. Serial sections of holotype. *3*, Combines a longitudinal transverse section of the extreme adoral end of the specimen with half of the cross section. *4*, Both halves of the cross section, the lower half identical with fig. 3. *5*, section 2 mm. farther apicad, shows the basal axis of the median septum, and the adoral tips of the endocones within the lateral cavities. *6*, Taken 7 mm. farther apicad, shows thicker endocones. *7*, The mirror image of fig. 6, shows the cones are thicker, the prongs of the septum are somewhat askew. Its axis is well shown, but it is not clearly differentiated from the endocones. *8*, section 30 mm. farther apicad; numerous thin cones are evident, but the center is somewhat recrystallized. *9*, The mirror image of fig. 8, lies at the adoral end of a portion of which a transverse longitudinal section was made. *10*, *11*, The two sides this longitudinal section. Note transverse lamellae in middle of fig. 10 crossing the axis of the septum. Endocones are visible in both figures; only in fig. 11 do they terminate in the tubes. *12*, Shows the axis of the septum, faint traces of endocones, and the beginning of the dark band connecting the numerous tubes now present; individual tubes are best seen on the left. *13–17*, Successive cross sections showing variations in the preservation of the tubes and the band connecting them, and the ultimate obscuring of the axis of the partition, poorly differentiated, but still present. Figures 17 and 19 lie at the ends of the section of fig. 18. Though longitudinal tubes are indicated here, the endocone boundaries so clear in figs. 10–11 are completely absent. The sections are approximately twice natural size. Middle Chazyan, Crown Point, New York. (p. 358)



Flower, Endoceroid classification



Flower, Endoceroid classification

normal to the axis of the siphuncle. Cross sections apicad of the tip of the endosiphocone show the line marking the tips of the cones as a prominent dark circular line. Within it are seen numerous small longitudinal tubes. There is some evidence of segregation of the tubes into groups around the periphery of the line, but the present material is insufficient to suggest any real symmetry in their arrangement. Likewise, there is no good evidence to indicate which side of the siphuncle is to be considered dorsal and which is ventral, though the triangular nature of the central pillar indicates a general bilateral symmetry.

Discussion.—This genus and species is so utterly unique among endoceroids that without evidence of septal structures on its outside, its nature as an endoceroid siphuncle might not have been suspected. The accompanying Text-fig. 6 suggests how this genus could be derived from the preceding one, and while some stages are hypothetical, at the present time no other possible relationship has been suggested by the present evidence. The unique and puzzling feature is, of course, the central pillar which grows forward in the siphuncle without, so far as the present incomplete specimen indicates, any visible means of support or any connection with the wall of the siphuncle. Were it not that the growth of the endocones which surround it completely, lag only very slightly behind it in development, the structure would be an absurdly and impossibly fragile one. It can, however, be derived from the median septum of *Allotrioceras* as suggested in the accompanying figure.

Text-fig. 6A–H represents the features already described for *Allotrioceras bifurcatum*. They have been adequately explained in the description of that genus, and are summarized in the explanation of the figure. The essential facts which must be kept in mind are as follows:

Allotrioceras begins its endosiphuncle by building a lining of the siphuncle from which a forked septum extends, almost completely dividing the siphuncle into two lateral parts. The area between the two prongs of the fork is filled later; no endocones are evident in its structure. The two lateral areas are, however, filled with endocones, modified in cross section in accordance with the section of the spaces they must fill. Adorally, dark bands distinguish the boundaries between individual conical elements. The cones on either side each terminate in a single lateral tube. Adapically, the boundaries of the cones fade and eventually dissappear. A dark line becomes apparent passing through the position of the angles of the cones on either side, the two sides continuing as a dark band and joining between the tip of the forked septum and the endosipholining. Instead of having a single tube in each half of the siphuncle, there are now several tubes in each half. They do not, however, appear to be present along the dark band as it extends across the middle of the siphuncle.

In typical *Allotrioceras*, it is evident that the anterior margin of the septum is curved, and not a plane, and that the forked tip extends slightly farther forward than the base of the septum, and much farther than the middle part of the septum. Text-fig. 6 I and J show progressive steps by which the pillar of *Mirabiloceras* can be derived from this septum. First the tip of the septum is prolonged forward. Second (J) with further prolongation, the two prongs of the fork tend to fuse so that a hollow space is completely enclosed by the fused prongs. Text-fig. 6K shows the inevitable result of the superposition of endocones upon such a

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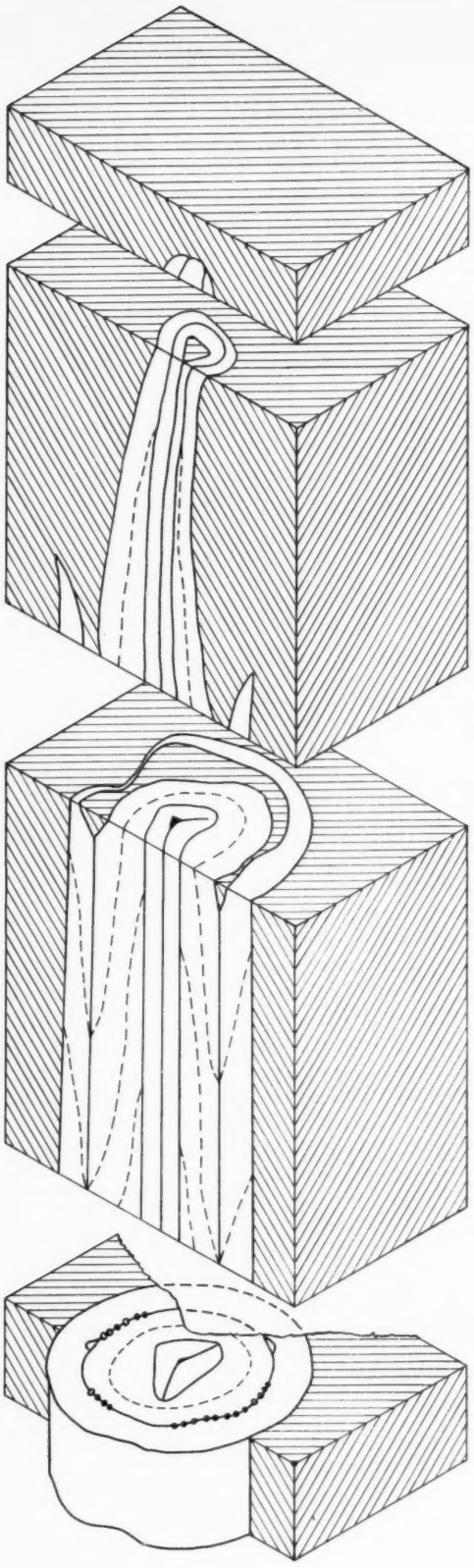
EXPLANATION OF PLATE 35

FIGS. *1–9*—*Mirabiloceras multitubulatum* Flower, n. sp. *1–2*, Longitudinal section, showing both exposed surfaces, slightly less than ×1. *3*, The same section shown in fig. 2, ×1.5. *4*, Cross section taken close to the base of the specimen, enlarged ×3 to show the endosiphotubes. *5*, The tubes shown in longitudinal section, the plane of the section longitudinal and tangential to the tubes, ×1.5. *6*, The central portion only of fig. 5, ×3. *7*, *8*, Two portions of the longitudinal sections preserving elements of the siphuncle wall. *9*, A retouched interpretation of the section shown in figure 8. (p. 364)



structure; the endocones will form a continuous circle around the central pillar.

The multiple tubes are unquestionably comparable to those noted in the early stages only of *Allotrioceras*. If one postulates cones superimposed upon the lower part of Text-fig. 6J, the result would be that shown in fig. 6L; the cones may be distributed in a line extending nearly around the siphuncle, but would be interrupted by the base of the septum. This condition differs from that of *Allotrioceras* mainly in that the prongs of the fork are shown here as nearly fused, and they lie in an essentially central position instead of close to one wall. When the cones grow forward close to the anterior end of fig. 6J, the pattern of the tubes could be continuous around the entire circumference of the central pillar, as shown in Fig. 6M. This is very close to the actual condition of *Mirabiloceras*. The incomplete nature of the cross section taken at the base of the type specimen makes it uncertain whether the segregation of the tubes into groups, not represented in the present figure, has any real accord with the symmetry of the siphuncle.

The end result is a seemingly paradoxical structure; the alignment of the inner limb of the endocone with the tip of the pillar gives this the appearance of a siphuncle in which the cones, instead of being pointed toward the apex, grew pointing toward the living chamber.

FIG. 5—Block diagram of the endosiphuncle of the holotype of *Mirabiloceras multitubulatum*. The central limb of the endocone extends nearly to the tip of the central pillar; the boundaries of the two are always distinct. The central pillar is hollow, shown in the uppermost cross section, becomes gradually filled, leaving only two lines running to the basal angles of its triangular cross section and a small central tube. The second cross section indicates that the tip of the endosiphocone is nearly at the same level around the periphery of the pillar; the irregularity in the outer limb of the cones is clearly a result of distortion. The basal section shows the dark band marking the position of the tip of the cone; the numerous endosiphotubes show some concentration in certain regions. Definite symmetry in their arrangement is not evident.

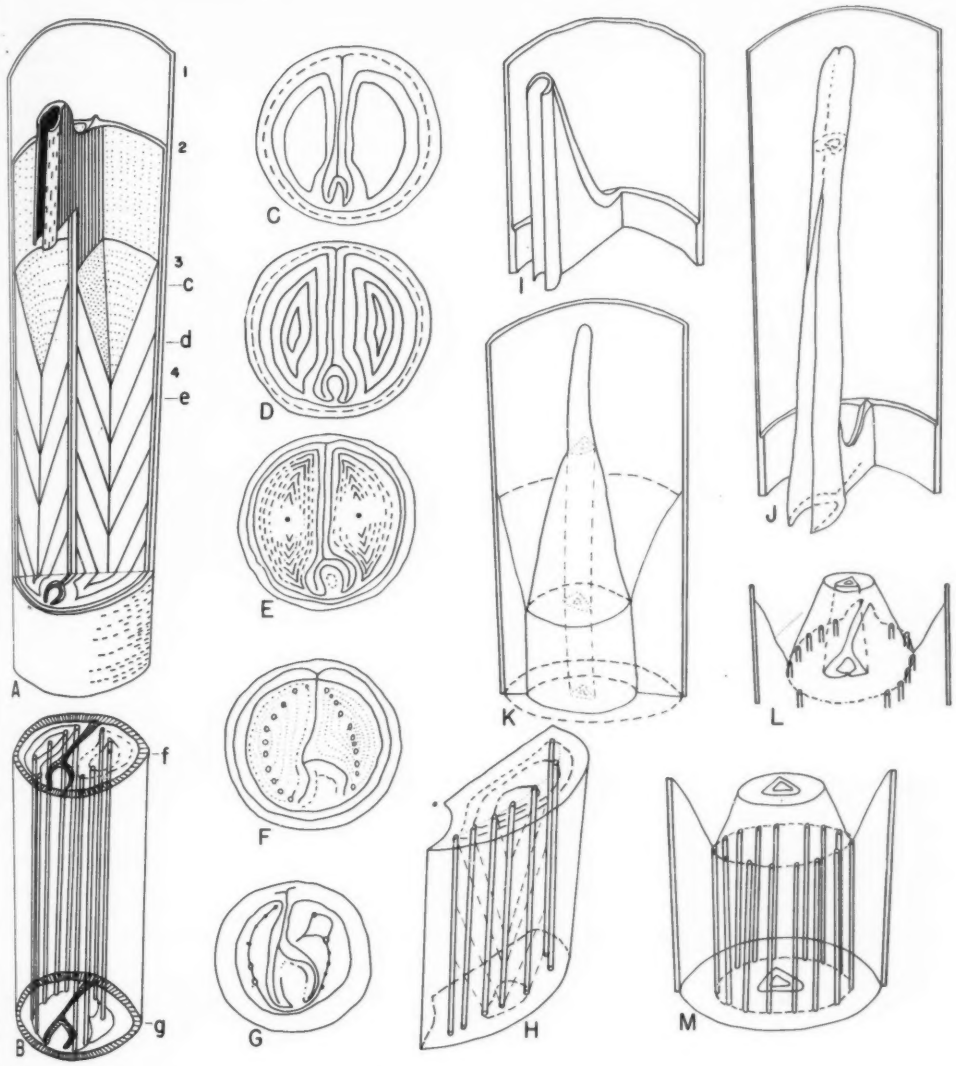


FIG. 6—Endosiphuncles of the Allotrioceratidae. A–H. *Allotrioceras bifurcatum*. A. Dissection of endosiphuncle. Successive growth stages are represented by (1) siphuncle wall (2) development of endosipholining, from which a septum with a forked tip extends nearly reaching the opposite side of the siphuncle. (3) adoral limit of last endocones, (4) tip of last endocones, terminating in paired lateral tubes. This interval is shown in a median horizontal longitudinal section, the tip of the forked tube cut away, and the front part of the whole siphuncle removed to the level of the two endosiphotubes. At the base, an oblique view of the remaining half of the cross section is seen, showing the forked tip of the septum and the boundaries of individual cones in cross section. Cones are actually somewhat more acute, longer, and more closely spaced than represented. B. Diagramatic representation of apical part of siphuncle. At the adoral end (f) margins of cones are still faintly indicated. Several tubes lie not only at the position of the two original endosiphotubes, but at intervals along a line joining the original tubes of the adoral portion with the angles of the endocones. Adapically (g), individual cones are no longer visible, but the tubes persist, and are joined by a prominent dark line. C. Cross section at c on Fig. 6A, showing lining, septum, and thin anterior

(*Continued on next page.*)

The cones of *Mirabiloceras* do not show clear dark lines separating individual endocones; for this reason, it is believed that growth of the cones was continuous and possibly fairly rapid. The implication of Fig. 6J that in the early part there may be a remnant of the basal part of the septum is misleading. There is of course no evidence as to whether such a condition does or does not exist; it is not essential to this explanation that it be retained in the ontogenetic stages. That figure shows the transition from the septum of *Allotrioceras* to the pillar of *Mirabiloceras* as an ontogenetic progression mainly as a matter of convenience.

MIRABILOCERAS MULTITUBULATUM
Flower, n. sp.
Pl. 35, figs. 1–9; Text-fig. 5

The essential features of the species are contained in the above description of the genus. It remains only to call attention to some details. The holotype is a small portion of a siphuncle. Its exterior is not visible; the specimen occurred in a black muddy limestone; the section shows that its surface was covered very largely by encrusting organisms. The endosiphuncle has a maximum length of 55 mm.. it is essentially circular in cross section. At the section taken close to its base the diameter is 24 mm. Adoral expansion is gentle, increasing in a section which is slightly off center from 23 to 25 mm. in the length of the outer wall, 25 mm.

Near its base, the longitudinal section of the siphuncle shows traces of the septa and connecting rings. The septa cannot be recognized. Repetition of similar elements, plainly representing the connecting rings, indicates that three camerae occupied a length of 10 mm. The appearance of the remnants of the siphuncle wall is shown in Pl. 35, figs. 7–9. There are clearly thick structures which are repeated, but which are well separated from one another. They are thicker on one side than on the other. Their texture indicates that they are connecting rings. Discrete rings are unknown in endoceroids. The ring extends from the tip of one septal neck to the tip of the next, or may be even longer, where the septal necks are invaginated, as shown in Text-fig. 1. The descrete rings can, then, be interpreted as remnants of invaginated siphuncles similar to those observed, and more clearly interpreted, in *Hudsonoceras*, and shown in Text-fig. 3. On the other hand, there are remnants of structure, very faint, in the portion shown in Pl. 34, fig. 8, which seem to be best interpreted as differentiation in rings outside of which lay very short septal necks. Although neither interpretation can be selected, the question is of such importance that it seems best to present in full the ambiguous evidence of the variable appearance of the sections.

The central pillar varies somewhat in cross section. In the basal section (Pl. 35, fig. 4), it is subtriangular, though somewhat distorted, the base of the triangle slightly concave. The section made just above the tips of the cones shows the triangular section more evenly, as indicated in Text-fig. 5, and a small triangular cavity in its center. A cross section near the anterior end shows a

endocones. D. Section at d on Fig. 6A, near tip of endosiphocones. E. Cross section at e on Fig. 6A; numerous endocones are more naturally represented here; their boundaries are becoming obscure, remaining strongest at the region of the angles. The two lateral endosiphotubes are strongly developed. F. Cross section at f on Fig. 6B; boundaries between cones are becoming faint; multiple tubes have developed. G. Cross section at base, at g of Fig. 6B. Outlines of cones have disappeared; remaining features show lining, forked septum, and dark band connecting the several endosiphotubes. H. Diagram of endocones on one side of septum, showing apparent relation between angles of cones and the multiple tubes. I–M. Hypothetical stages leading from *Allotrioceras* to *Mirabiloceras*. I, J. Progressive stages in the anterior extension of the forked tip of the median septum. It is projected forward simply in I; in J the extension is increased, and at the anterior end the prongs of the fork join enclosing a central space. This ontogenetic progression is not demonstrated; in K cones develop around the periphery of the central pillar developed in the adoral end of J. L. Basal portion of last endocones only, showing cross section of the pillar, and, basally, its theoretical continuation as a septum. Endotubes are still concentrated on the two lateral areas. M. A section similar in position to that of L, but showing the condition of typical *Mirabiloceras*. The lining and septum are suppressed; cones continue without interruption around the central pillar, the tubes numerous and potentially evenly distributed.

wider central cavity, but the exterior of the pillar is more rounded in cross section. The central cavity must have been open to the anterior growing surface.

The fact that the central pillar is slightly askew in the longitudinal sections shown, and that the endocones are deeper on one side than on the other, suggests a bilaterally symmetrical pattern. A cross section taken just above the tip of the endosiphocone was made but, as shown in Text-fig. 5, evident distortion made it impossible to come to any definite conclusions, other than that the central pillar had essentially the section of an isosceles triangle, short and with a broad base, but it proved impossible to say whether its base or apex should be considered as marking the ventral side.

The dark band marking the position of the apex of the endocone which extends around the circumference of the pillar, shows numerous tubular elements, shown in detail in Pl. 35, fig. 4. Farther orad a section was taken tangential to this conical surface. At an early stage, the tubes were continuous throughout the length of the section. Further grinding removed their middle portions in attempting to smooth down the section for photography. Nevertheless, the nature of these structures as tubes seems beyond question. It should further be noted that while the pillar is always distinctly set off from the endocone around it, within the endocone there can be seen no clear dark bands indicating individual conical elements as in many endoceroids, leading to the conclusion that deposition of the endosiphuncle in this form was probably essentially continuous.

Discussion.—This species is so utterly alone in the characters of the endosiphuncle that there is nothing else with which it can be confused. There always remains the possibility of course that it might prove to be conspecific with endoceroid species described from anterior parts of the shell and showing nothing of the endosiphuncle. In this case the danger is remote. Endosiphuncles of all of the described species from the Chazyan of the Champlain valley have been observed, except for *Endoceras magister* Ruedemann, which is obviously not nearly closely septate enough to be conspecific with the present form.

Occurrence.—This specimen is derived from a loose block from the north side of the bay on the southeast corner of Valcour Island immediately north of Cystid Point. Similar material in place there leaves no doubt but that it originated where it was found. Curiously, this layer of rubbly muddy limestone contains many endoceroid siphuncles, but none of the other specimens collected show other than the typical pattern of endocones. The holotype is in the collection of the writer.

OUTLINE OF CLASSIFICATION OF THE ENDOCERATIDA

Family PROTEROCAMEROCERATIDAE Kobayashi, emend. Flower

Shells slender, largely straight, but sometimes endogastric cyrtocones. Siphuncle of concave or tubular segments, usually close to venter; septal necks typically short, but showing all stages from aneuchoanitic (achoanitic, Teichert and Glenister, 1954) to hemichoanitic and subholochoanitic. Endosiphuncles generalized in older genera, but becoming immensely specialized in others in section of cones, position of tube number and arrangement of blades.

The known features of the genera are presented only in summary form.

Proendoceras Flower, n. gen. Shells similar to *Pachendoceras* in broad cross section, simple stuures, and apex; septal necks achoanitic in young, may be hemichoanitic in adult. Endosiphuncle generalized. Middle and possibly upper Canadian.

Clitendoceras Ulrich and Foerste. Cross section circular or compressed; sutures slope forward on dorsum; shell slightly endogastric; isolated siphuncles slender and markedly curved. Septal necks short in young, lengthening in adult. The later endocones are projected far forward on the ventral side; the speiss showing some ventral flattening. The genotype, *C. saylesi* is not from the Fort Cassin beds as stated, but from the middle Canadian beds with *Lecanospira*. Species range from equivalents of the Roubidoux to beds of Powell age.

Cyptendoceras Ulrich and Foerste. Shell straight, slender, cross section depressed. Sutures with ventral and sometimes dorsal lobes. Siphuncle ventral, wall structure unknown. Pattern of endosiphuncle not de-

termined. Known species range from the Jefferson City to the Powell formations.

Cyptendocerina Ulrich, Foerste, Miller, and Unklesbay. Sutures with ventral lobes as in *Cyptendoceras;* shell more rapidly expanding, siphuncle smaller, somewhat removed from venter. Siphuncle wall structure undetermined. The endosiphuncle is unknown; consequently the genus is not even demonstrably a member of the Endoceratida. The type species is the only one which has been referred to this genus. It is from the boulders of the Levis conglomerate.

Manitouoceras Ulrich, Foerste, Miller and Unklesbay, is known only from isolated siphuncles, fairly large slender, straight adorally, the venter slightly convex near the blunt apex. Siphuncle wall unknown. Cones reported as circular, terminating centrally, slender. The blades, previously unreported, appear to be three in number, but preservation is poor in the type material.

Kirkoceras Ulrich and Foerste is based upon isolated slender slightly curved siphuncle. Siphuncle wall unknown. Cones terminate in a central tube. Poor preservation makes the number and position of blades, ambiguous in the type material. Siphuncles circular or compressed in cross section. Particularly characteristic of a Roubidoux horizon in the Manitou and El Paso "formations."

Oderoceras Ulrich, Foerste and Miller, 1943, is based on isolated curved siphuncles differing from *Kirkoceras* mainly in the broader depressed cross section. Siphuncle wall unknown. The descriptions tell nothing about the endosiphuncles. Isolated siphuncles of both *Kirkoceras* and *Oderoceras* are very similar to siphuncles dissected from *Clitendoceras.* I had for some time regarded the genera as doubtfully distinct. *Kirkoceras,* at least possesses blades not found in *Clitendoceras,* and apparently lacks the ventral prolongation of the last endocones.

Utoceras Ulrich, Foerste and Miller, 1943, is based upon relatively large, slightly curved siphuncles. They probably represent the slender adoral parts of siphuncles of piloceroids.

Oelandoceras Foerste, 1932, is a compressed curved shell. The ventral siphuncle has short septal necks. On this basis it was formerly placed in the Proterocameroceratidae (Flower and Kummel, 1950) but endocones have not been demonstrated, and the genus may be referable instead of the Ellesmeroceratida.

Proterocameroceras Ruedemann, 1905. Shell straight, sutures simple, siphuncle ventral, necks short, forked, ring thick and layered (Flower, 1941) endosiphuncle highly specialized (Ruedemann, 1905) with semicircular cones and three blades. The apex of the shell is supposed to contain only the siphuncle, the appearance of camerae being somewhat delayed. This genus is more widespread in the Canadian of America than was previously believed. *Mcqueenoceras franklinense* Ulrich, Foerste, Miller and Unklesbay (1944) shows the essential features of endosiphuncles of the genus.

Mcqueenoceras Ulrich and Foerste is a slender shell, slightly curved to straight, differentiated from *Clitendoceras* by the position of the tube close to the dorsal wall of the siphuncle. Cones are produced ventrally, the surface strongly flattened. Blades have not been observed, nor has the structure of the siphuncle wall. The endocone is similar to that of *Proterocameroceras* except for the markedly dorsal termination. It is probably closely related to both of these genera. *Mcqueenoceras* is very characteristic of a horizon of early Jefferson City age.

Anthoceras Teichert and Glenister, 1954, is an annulated endoceroid, the endocones simple, the septal necks three fourths the length of a camera in the adult. Blades not observed. Canadian of Australia and North America.

Campendoceras Teichert and Glenister, 1954, is a small annulated slender faintly endogastric endoceroid. Necks are subholochoanitic; cone terminating centrally and apparently simple. Blades unknown, probably not developed. Upper Canadian of Australia.

Meniscoceras Flower, 1941. Shell surface and suture pattern unknown. Necks short. Paired lateral blades curve from the dorsolateral wall to cones, semicircular, flattened dorsally, or tube. A median dorsal blade is present. Known only from the middle Chazyan. Neuman (1951, pl. 7, fig. 24), has figured a cross section of a siphuncle of

this genus from the Row Park limestone of Pennsylvania as a *Beatricea*.

Family ALLOTRIOCERATIDAE Flower

This family, described in the preceding pages, contains only the two new genera *Allotrioceras* and *Mirabiloceras*. For reasons discussed, it is regarded as derived from the Proterocameroceratidae through *Meniscoceras*.

Family MANCHUROCERATIDAE Kobayashi

Siphuncles with the endocones forming a convex mass on the ventral side; in specialized forms the ventral mass is set off by a pair of prominent blades. Septal necks vary from very short to very long.

Manchuroceras Kobayashi (=*Liaotungoceras* Shimizu and Obata and *Grabauoceras* Shimizu and Obata) is based upon rather large siphuncles, of piloceroid aspect, but depressed in cross section. Lateral blades not well developed; tube crossed by diaphragms. Wolungian (upper Canadian) of eastern Asia. Some sections indicate a midventral blade. Kobayashi attributes to this genus a ventral alveolus.

Coreanoceras Kobayashi is based upon smaller more slender siphuncles. The septal neck is known to be very short. Ventral mass set off by prominent lateral blades, sometimes double. Alveolus reported; midventral blade sometimes indicated. Endocones strongly crescentic in section. Upper Canadian of eastern Asia and America.

Hudsonoceras, described above, differs from *Coreanoceras* in the large size and very slender shell, the septal necks which extend for one and a half camerae, the transverse bands crossing the endosiphuncle at regular intervals, the faint but more numerous secondary endosiphoblades. Chazyan of North America.

Family CHIHLIOCERATIDAE Grabau

Known only from a short broad siphuncle of piloceroid aspect, which is divided into a primary central endocone and two lateral cones. Known from the Canadian of North China, the remarkable genus *Chihlioceras* has not generally been believed. It becomes more credible after studying the Allotrioceratidae.

Family PILOCERATIDAE S. A. Miller

Shells rapidly expanding in the young, siphuncle also very rapidly expanding, leaving often only very restricted camerae. Adorally the siphuncle and shell may both become more slender; mature living chambers may be tubular or contracted at the aperture. Cross section of shell and siphuncle compressed. Siphuncle wall where known, holochoanitic. Endocones generally simple in cross section, but blades or funicles may become complex. Tubes sometimes crossed by diaphragms. The genera as at present delimited are recognized primarily by form. *Piloceras* is cyrtoconic, the siphuncle evenly and moderately expanding. *Cassinoceras* has a very large siphuncle, nearly straight except near the apex which may be relatively slender. The siphuncle of *Allopiloceras* is very rapidly expanding in the early portion, becoming much more slender adorally. As noted, *Utoceras* is probably based on adoral portions of siphuncles of true piloceroids. A revision of the group will be involved in the description of the faunas of the El Paso limestone which contains a remarkable concentration of true piloceroids.

Family ENDOCERATIDAE Hyatt

Straight slender endoceroids, often large, siphuncle wall holochoanitic throughout; endocones remain relatively simple in cross section; siphuncle primitively swollen at apex, the swelling reduced and lost in more specialized forms.

Endoceras.—As outlined above, *Endoceras* is still a very broad genus, section circular or depressed, sutures simple, siphuncle large, close to the venter in most species, cones typically circular, terminating in the ventral part of the siphuncle, but other types of cones are at present included in the genus. Early stages certainly include those named *Cameroceras*, and also *Nanno*, and *Suecoceras*. Chazyan to Richmond.

Vaginoceras.—As discussed above, distinguished from *Endoceras* by the compressed cuneate cone, central tube supported by a dorsal and a ventral blade. Siphuncle wall similar to *Endoceras*, but with connecting rings unusually thick.

Cyclendoceras Grabau and Shimer, 1910, is an annulated affine of *Endoceras*, based upon *Endoceras annulatum* of the lower Trenton of New York. Siphuncle wall as in *Endoceras;* endosiphuncle not studied. The genus is known to range from the Lowville to the Red River faunas of doubtful Richmond age.

Kotoceras Kobayashi, 1934, is a relatively large slender endoceroid, cross section slightly depressed, siphuncle wall holochoanitic, siphuncle depressed in cross section, in flattened ventral contact with the shell. Endocones extend much farther forward on the venter than on the dorsum. Speiss semicircular to obscurely subquadrangular in cross section; cones thin on middorsal region. The genus is known only from the Toufangian of Manchuria. A related type, but apparently a distinct genus, has been found in the Chazyan of eastern North America.

Kawasakiceras Kobayashi, 1934, is regarded as distinguished from *Kotoceras* by the annulated surface of the shell. Necks are apparently holochoanitic. The features of the endosiphuncle are not known.

Dideroceras Flower. Slender endoceroids with rather deep camerae in proportion to the shell diameter. Siphuncle ventral, septal necks extending for the length of two camerae, rarely one and a half. Endocones simple, their termination subcentral. Blades have not been observed. Apical ends are believed to belong to the *Nanno* type, but further confirmation is required. Upper red and grey *Orthoceras* limestone of Europe and Asia.

Chisiloceras Gortani differs from *Dideroceras* in the central rather than ventral siphuncle. On this basis the genus was originally described, and separated from *Vaginoceras,* to which were attributed the features of *Dideroceras.* Upper *Orthoceras* limestone equivalents of southeastern Asia.

Cyrtendoceras Remelé is inadequately known internally. It is a strongly curved shell, evidently gyroconic when complete, slender, compressed in cross section. Both siphuncle and shell are quite slender. The siphuncle wall is identical with that of *Endoceras.* There is good indication of endocones, but their cross section, the position of the tube, and the blades if any, are unknown, as is the condition of the initial part of the shell. True *Cyrtendoceras* is confined to the upper grey *Orthoceras* limestone. Older species attributed to the genus almost certainly belong elsewhere.

Genera of Endoceratidae Based on Early Stages

The genus *Cameroceras,* as discussed above, is certainly the early portion of a number of species of *Endoceras* including the genotype. Sardeson (1930) also considered *Cameroceras* to be the early stage of *Endoceras annulatum.* If so, early stages of typical *Cyclendoceras* have been included.

Nanno Clarke is an early stage in which the siphuncle completely fills the apical part of the shell, and is then constricted as shown in Text-fig. 2 A–D. It ranges from Chazyan to Richmond. The siphuncle wall of *Nanno aulema* has not been analyzed; that of *Nanno noveboracum* is holochoanitic. *N. noveboracum* is the early stage of "*Vaginoceras*" *oppletum.* Sardeson (1925) identified *N. aulema* with what is now *Endoceras clarkei* Miller and Kummel (1944).

Suecoceras Holm is known only from the *Orthoceras* limestone of northern Europe. It also appears to be the initial part of shells, the adult parts of which are typical *Endoceras.*

Foerstellites Kobayahi, based upon *Endoceras faberi* Foerste, has the swelling of the apical end of the siphuncle suppressed. It is the early stage of an undescribed species of *Endoceras* in the Whitewater and Saluda. It is suspected that the early stages of *Vaginoceras* are quite similar, on the basis of topotype material. It is of interest to note that Whiteaves (1905, p. 24, pl. 2, fig. 1) figures the apical part of such a siphuncle from the Paquette Rapids, which presumably belongs to *Vaginoceras,* since only that genus has been recognized there on the basis of later portions of siphuncles.

Inadequately Known Genera Probably Belonging to the Family Proterocameroceratidae

Previous experience indicates that quite probably the slender endoceroids of the Canadian can be assigned to the Proterocameroceratidae. The genera included under

that family have not all yielded siphuncle walls for study, but apparently form a closely knit group. The following genera of the Canadian probably belong there, but the evidence is regarded as less conclusive:

Tasmanoceras Teichert and Glenister (1952) of the Canadian of Tasmania, is known from isolated siphuncles unique in endoceroids in being broadly expanded between the septa. Siphuncle wall not observed. Tube slightly dorsad of center, cones steeper and much farther prolonged orad on the venter than on the dorsum.

Allocotoceras Teichert and Glenister (1953) is a small slender endosiphuncle with the crescentic endocone oriented the reverse of that of *Coreanoceras* and *Kotoceras*, but similar to that of the more complex *Meniscoceras*.

Genera of Piloceroid Aspect

Some generic names have been based upon siphuncles which are rapidly expanding and therefore of piloceroid aspect. Information is inadequate to determine their precise position; usually little is known of their structure. They include *Penhsioceras* Endo, *Subpenhsioceras* Shimizu and Obata, *Hemipoloceras* Shimizu and Obata, and *Lingchengoceras* Obata (1940).

Mysticoceras Ulrich and Foerste (see Ulrich, Foerste, Miller and Unklesbay, 1944) is known only from apical parts of siphuncles which are short, rapidly expanding, show strongly inclined septal markings, and contain relatively large spicula, suggesting that either the specimens are immature, or that the species never developed a long endosiphuncle. It is known only from the Hastings Creek formation of the Phillipsburg region of Quebec. It is probably the early part of the siphuncle of a relatively large endoceroid, and probably belongs in the Proterocameroceratidae. Early stages of other members of the Proterocameroceratidae have been found showing similar proportions, though on a somewhat smaller scale. An allied species, also known only from an endosiphuncle, awaits description from the middle Canadian of Maryland. The genus is neither a true piloceroid, nor is it related to *Suecoceras*. Indeed, the family Suecoceratidae of Shimizu and Obata (1936) is not a natural group. *Suecoceras* is one of several types of early stages found in typical Endoceratidae.

Post-Canadian Genera

Here are summarized some inadequately known genera of Chazyan or younger age. Their position as members of the Endoceratidae, or as possible derivatives of other lines, is still highly uncertain in the light of the very incomplete information available. Some are, however, characteristic and recognizable in themselves, and good generic groups.

Paravaginoceras Kobayashi (1934). All that is known of this genus is portions of endosiphuncles, depressed in cross section, and with a central tube. Cones are presumably slender, but inadequately shown. Toufangian of eastern Asia.

Cyrtovaginoceras Kobayashi (1934) was erected for slightly curved endoceroids apparently of the Endoceratidae. While the need for a separate genus for such very slightly curved forms is dubious, the type species, *Cameroceras curvatiformis*, is a highly characteristic siphuncle which cannot be placed in any other generic group. The shell is slightly curved, the apex slender for an interval, then becoming rapidly expanding. The increase in expansion happens to occur in some specimens at the level of the tip of the endosiphocone. A shell of this type was made the basis of *Trifurcatoceras* Obata (1940). Probably a later growth stage of the same or a similar species was named by Obata (1940) as *Endoceras hayasakai*, and his *E. yabei* is also congeneric. I regard the genus as significant, having collected similar siphuncles in the middle Chazyan of New York. They are undescribed, but rest in the New York State Museum.

None of the known material shows the structure of the siphuncle wall. Sections of the New York material have shown only an indication of a subcentral tube; the remainder of the siphuncle was strongly recrystallized.

Genera regarded as endoceroids but otherwise unrecognizable, include *Sidemina* Castlenau, *Sannonites* Fischer de Waldheim, *Colpoceras* Hall, *Diploceras* Conrad, *Conoceras* Bronn, *Kaipingoceras* Shimizu and Obata, *Neokaipingoceras* Obata.

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MISSISSIPPIAN PLANT SPORES FROM THE HARDINSBURG FORMATION OF ILLINOIS AND KENTUCKY

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ABSTRACT—Plant spores from core samples of three wells and five outcrop samples of the Hardinsburg formation of Upper Mississippian age from Kentucky and Illinois are described. The spore assemblage consists of 19 genera including three proposed as new, and 59 species of which 37 are new. The difference in the technique employed in the maceration of carbonaceous shale from that in the maceration of coal is discussed. Literature on Mississippian spores is meager and vague, as the few articles concerning spores of this age refer to coal seams which have not been definitely correlated with type Mississippian sections.

New genera described are *Auroraspora*, *Convolutispora* and *Grandispora*. New species described are *Acanthotriletes echinatus*, *Apiculati-sporites pineatus*, *Auroraspora solisortus* (genotype), *Cirratriradites granulatipunctatus*, *C. praetergranulatus*, *C. uber*, *Convolutispora ampla*, *C. florida* (genotype), *C. mellita*, *C. tesselata*, *C. venusta*, *Denso-sporites brevispinosus*, *D. capistratus*, *D. parvus*, *D. spinifer*, *D. tenuis*, *Endosporites endorugosus*, *E. minutus*, *Grandispora spinosa* (genotype), *Granulatisporites politus*, *G. tuberculatus*, *Knoxisporites rotatus*, *K. triradiatus*, *Microreticulati-sporites fundatus*, *Punctati-sporites baccatus*, *P. cerosus*, *P. fissus*, *P. grandis*, *P. nitidus*, *P. plicatus*, *P. pseudolevatus*, *P. reticulopunctatus*, *P? callosus*, *Raistrickia multipertica*, *Reticulati-sporites decoratus*, *Schulzospora elongata*, *Triquitrites marginatus*.

INTRODUCTION

THE use of fossil spores and pollen is an important tool in oil exploration, both as a near-shore indicator and as a time marker in the stratigraphic column. Their small size, abundance, and ease of recovery from indurated rocks (outcrops, well cores and cuttings) give these fossils increased utility in comparison with other microfossil groups.

The objectives in writing this paper are to describe criteria for the separation of Upper Mississippian sediments from those of the Lower Pennsylvanian on the basis of plant spores and to point out the present confused status of fossil spore taxonomy.

Several systems of spore classification are being used by workers in different parts of the world. The resulting confusion in spore nomenclature is discussed in the section on taxonomy. The authors have adopted a conservative view, and have avoided the creation of new names at the generic level unless unmistakable new and distinct characteristics were evident. Several previously erected form genera based on the nature of spore coat processes grade into each other and the assignment of species to these genera is therefore difficult. In such cases, the species have been assigned to broadly definied form genera which have been recognized by most American workers.

Literature covering Mississippian spores is scarce and inadequate. In addition, literature on Paleozoic spores is restricted largely to assemblages from coal seams. Coals generally contain the best preserved spores, but represent a limited environment of deposition and form only a small percentage of the total rock column. An examination of several thousand samples from widely scattered areas in the United States and abroad indicates that most carbonaceous shales yield abundant well-preserved spores and pollen. Spore and pollen assemblages from clastic lithologies are more representative of the lithologies included in a formation. Population counts of spores and pollen from shales overlying and underlying a coal seam are more indicative of the broader aspects of the ancient flora than those made from the coal.

Shales and coals of the Hardinsburg for-

mation, Chester series, Upper Mississippian of Illinois and Kentucky were found to contain a large and varied spore assemblage. Many of the species and genera do not occur in Pennsylvanian strata, and with few exceptions, the Hardinsburg species do not occur in the overlying Pennsylvanian coals of Illinois from which spore assemblages were described by Kosanke (1950). Three new genera and 37 new species are proposed here and several new spore types, imperfectly understood at this time, are recorded.

Hardinsburg core samples from three wells and samples from five outcrops in Kentucky and Illinois were studied (Text-fig. 1). The well sections (Text-fig. 2) were identified by geologists of The Carter Oil Company as Hardinsburg. The outcrop samples, supplied at the request of Dr. A. C. McFarlan, Director of the Kentucky Geological Survey, were collected and identified as Hardinsburg by Edmund Nosow of the Kentucky Geological Survey. A few of the spores were also identified from samples of the somewhat younger Waltersburg formation in Illinois. The position of these two formations in the standard Upper Mississippian section is indicated in Text-fig. 2. The writers wish to thank The Carter Oil Company for permission to publish this article, and McFarlan and Nosow for their help.

OUTCROP AND WELL LOCATIONS
(See Text-figs. 1, 2)

Hardinsburg formation

TCO-82—Carter No. 3 M. Tapp, 19-N-23 (Carter Coord.), Bald Knob Field, Webster County, Kentucky, 2071.5–2089 feet. Samples prepared of material from 2071.5, 2072, 2075, 2076, 2077, 2078, 2079.4, 2081, 2081–84, 2085, 2086, 2087, and 2087–88 feet.

TCO-153—Carter No. 1 J. E. Horn, NW NE SW 8-8S-7E, Eldorado Pool, Saline County, Illinois. No. 1, 2325 feet (coal); No. 2, 2324.9 feet; No. 3, 2325.1 feet.

TCO-158—Lee Reich No. 1, SW SW NE 8-8S-7E, Eldorado Pool, Saline County, Illinois, 2305 feet (shale), and 2309 feet (coal-bearing shale). Well elev. 378 feet.

TCO-143—Kelly quadrangle, Christian County, Kentucky. No. 1. River Bottom 1000–2000 feet west of lake draining into Tradewater River, 15-F-25 (Carter coord.) No. 2. Same as above. No. 3. Tributary valley of Middle Branch of West Fork of Pond River, SE of 1-F-25 (Carter coord.) No. 4. Just south of dam at Lake Morris, 1350 feet S line, 1500 feet E line, 23-F-25 (Carter coord.) No 5. Same as No. 1.

Waltersburg formation

TCO-108—Inland Producing Co., No. 3 Pielemeier, NE NE SE 28-8S-10E, Gallatin County, Illinois, 1993–1995 feet.

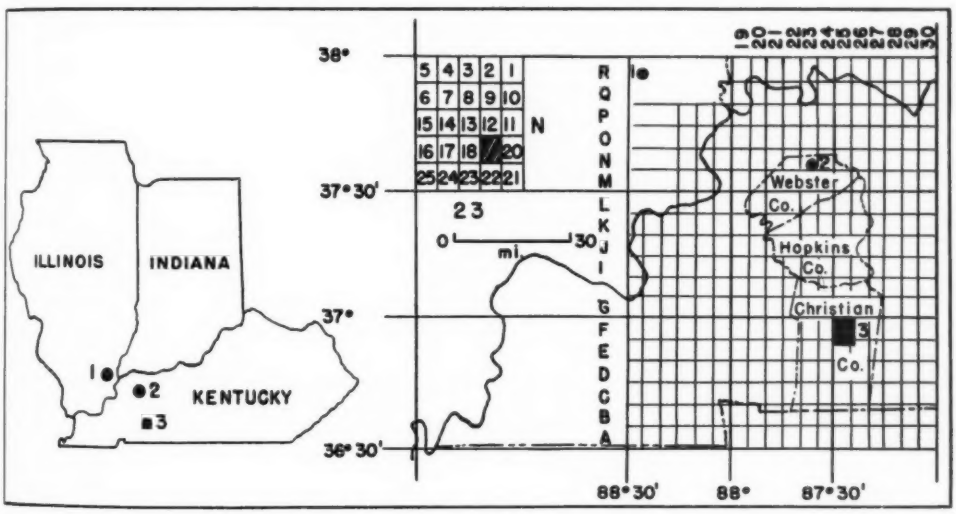

FIG. 1—Index map of Hardinsburg formation localities. 1. Carter No. 1, J. E. Horn (TCO-153) and Lee Reich No. 1 (TCO-158), Saline County, Illinois. 2. Carter No. 3 M. Tapp (TCO-82), Webster County, Kentucky. 3. Outcrop area (TCO-143), Kelly Quadrangle, Christian County, Kentucky.

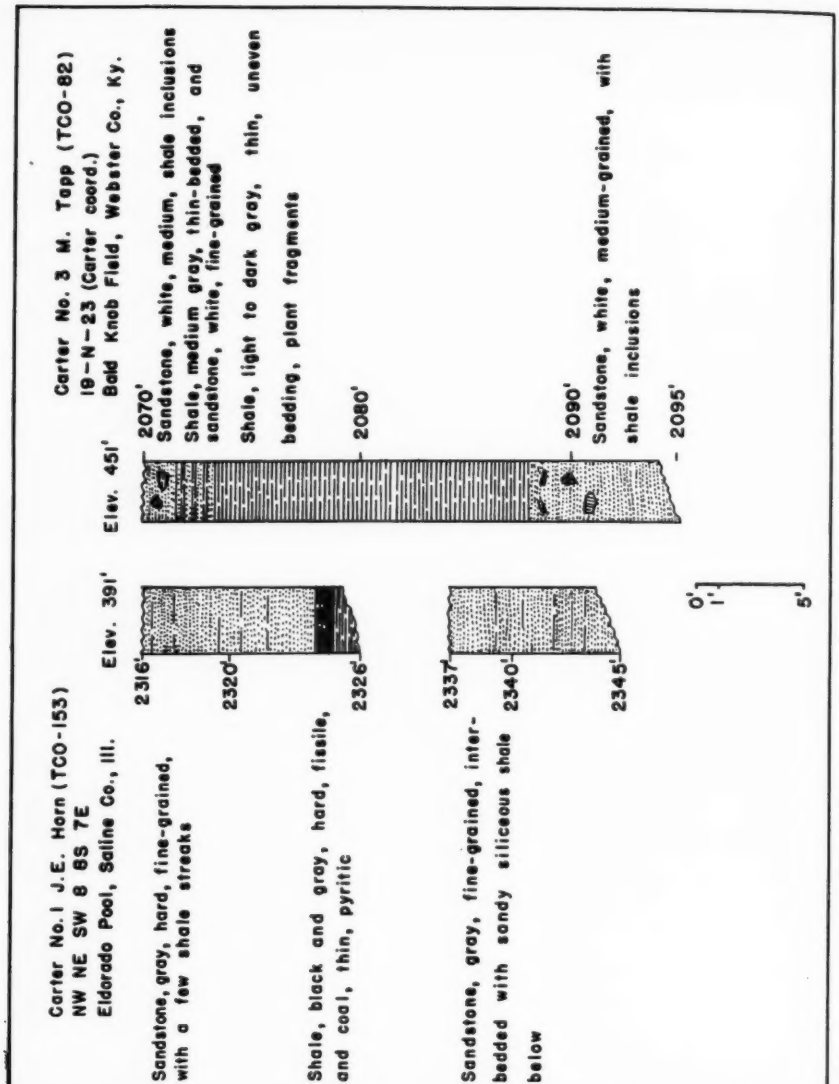

FIGURE 2. STANDARD UPPER MISSISSIPPIAN (CHESTER) SECTION AND LITHOLOGIC DESCRIPTIONS OF SAMPLED WELL INTERVALS

METHODS

Spore separation techniques for coals and carbonaceous shales have been discussed by Wilson (1946) and Kosanke (1950). Briefly, the shale samples are broken into $\frac{1}{8}$–$\frac{1}{4}$ inch fragments, covered with 52 percent hydrofluoric acid in a copper beaker, and allowed to digest 12 to 18 hours. The samples are then brought nearly to the boiling point, diluted with distilled water, and centrifuged. Dilution and centrifuging are repeated several times. The washed residues are transferred to small beakers, mixed with warmed glycerine jelly, and placed in a dessicator for approximately 16 hours. Permanent slides are prepared from the rewarmed glycerine jelly mixtures. Diaphane or balsam may also be used.

Coal samples are crushed into fragments as above, oxidized in Schulz' solution (two parts concentrated nitric acid, one part saturated potassium chlorate solution), diluted with distilled water, centrifuged several times, and the washed residue treated with 5 percent potassium hydroxide. The samples are then washed and centrifuged, mixed with cellosolve, and recentrifuged. The residues are mixed with diaphane and permanent slides made from the preparation.

The slides are studied and photomicrographs taken at 800×. Statistical counts of the microfossils in each sample are made to determine relative abundances.

PREVIOUS LITERATURE ON MISSISSIPPIAN PLANT SPORES

W. Berry (1936), in a paper on the Pennington coal of Tennessee, first reported on Mississippian spores of the United States. Schemel (1950) described a number of species from a Lower Carboniferous coal of Utah. Neither coal, however, has been correlated satisfactorily with type Mississippian sections. Luber and Waltz (1938) described many species from the Tournaisian and Viséan coals of the U.S.S.R. Raistrick (1938) and Knox (1948) illustrated forms from the Lower Carboniferous Limestone coal group of Scotland and Northumberland, but did not formally describe genera and species.

SPORE ASSEMBLAGES OF THE HARDINSBURG FORMATION

Nineteen genera of plant spores, including three proposed as new, are described. The new genera are *Auroraspora*, *Convolutispora*, and *Grandispora*. The most abundant genera, constituting 95 percent or more of all spores in the samples, are *Cirratriradites*, *Punctati-sporites*, *Denso-sporites*, *Granulati-sporites*, and *Schulzospora*. *Cirratriradites* averages 40–50 percent of all spores in each sample with the exception of coals from the Carter No. 1 Horn and No. 1 Lee Reich (See Table 1).

In Carter M. Tapp No. 3 only slight variations occur in the relative abundance of the genera at different levels in the 16 feet of shale section. *Denso-sporites* is more abundant and *Granulati-sporites* less abundant in the middle of the section. The spore assemblage of the coal from Carter No. 1 Horn is significantly different from those of the immediately super- and subjacent shales; *Cirratriradites* averages about 85 percent in the coal and about 50 percent in the shales. *Punctati-sporites* is more abundant in the shales than in the coal, and *Denso-sporites*, *Acanthotriletes*, *Apiculati-sporites*, and *Calamospora* are more common in the coal. Small alete bodies of unknown affinities average 40 percent of the forms in the coal. *Denso-sporites* constitutes 30 percent of the spores in a coaly shale (2305 feet) from the Hardinsburg in the Lee Reich No. 1 well, which is located in the same section as the Carter No. 1 J. E. Horn. Four feet above the coaly shale *Cirratriradites* is the most abundant spore.

With the exception of one sample, *Cirratriradites* averages 45–55 percent and *Punctati-sporites* 30–35 percent of the spores from samples of shales exposed in Christian County, Kentucky. These figures compare well with the results for the cored shales although the spore florules of the outcrop samples are less varied. Marine microfossils are common in the outcrop area (Edmund Nosow, personal communication), therefore, fewer spores would be expected. At TCO-143 No. 3, small alete forms (cysts?) average 39 percent and *Cirratriradites* and *Punctati-sporites* average respectively 29 and 21 percent. If the percentages are cal-

culated excluding the aletes, no differences in relative abundance exist between this sample and the other outcrop samples.

A coal-bearing shale sample (core) from the Waltersburg formation of the Chester series (TCO-108, Gallatin County, Illinois), examined for comparative purposes only, possesses *Cirratriradites*, *Schulzospora*, and *Punctati-sporites* in equal abundance.

Relative generic abundances may change considerably within short stratigraphic intervals in the Hardinsburg formation, suggesting environmental differences, although the genera and species are essentially the same.

MISSISSIPPIAN SPORE ASSEMBLAGES

Denso-sporites constitutes 92 percent of the spores while *Cirratriradites* is absent in a coal of probable Upper Mississippian age from Daggett County, Utah (Schemel, 1950). A few species (*Tripartites vetustus*, *Endosporites pallidus*, *Rotaspora fracta*) are common to the spore florules of this coal and the Hardinsburg formation. The general aspect of spores from Tournaisian-Viséan coals of the U.S.S.R. (Luber and Waltz, 1938) is similar to that of the Hardinsburg formation. *Schulzospora*, *Denso-sporites*, *Cirratriradites*, *Tripartites*, *Convolutispora* n. gen., possibly *Auroraspora* n. gen. and possibly *Knoxisporites* are present in both regions. In the Limestone coal group of Scotland and Northumberland, *Triquitrites*, *Cirratriradites*, and *Convolutispora* n. gen. are present, but data are not available on the relative abundance of these or other genera.

Laevigato-sporites is rare or absent in Mississippian rocks. The genus *Tripartites* seems to be restricted to Mississippian

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EXPLANATION OF PLATE 36

FIG. *1*—*Punctati-sporites reticulopunctatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 53×57 microns. (p. 394)

2—*Punctati-sporites? baccatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 29 microns. (p. 392)

3—*Microreticulati-sporites fundatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 27×29 microns. (p. 391)

4—*Punctati-sporites nitidus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 34 microns. (p. 393)

5—*Punctati-sporites pseudolevatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 61 microns. (p. 394)

6—*Punctati-sporites? cerosus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 48 microns. (p. 392)

7—*Punctati-sporites grandis* Hoffmeister, Staplin and Malloy, n. sp., holotype size 120 microns. (p. 393)

8—*Punctati-sporites fissus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 57×61 microns. (p. 393)

9, *10*—*Punctati-sporites plicatus* Hoffmeister, Staplin and Malloy, n. sp.; *9*, holotype, size 38×43 microns; *10*, size 32×36 microns. (p. 394)

11—*Granulati-sporites* cf. *G. pallidus* Kosanke, 1950; size 38 microns. (p. 389)

12—*Granulati-sporites tuberculatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 41.5 microns. (p. 389)

13—*Granulati-sporites politus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 37.5 microns. (p. 389)

14, *15*—*Denso-sporites capistratus* Hoffmeister, Staplin and Malloy, n. sp.; *14*, size 53 microns; *15*, holotype; size 41×46 microns. (p. 386)

16, *17*—*Denso-sporites spinifer* Hoffmeister, Staplin and Malloy, n. sp.; *16*, size 37.5×31.5 microns; *17*, holotype, size 42×46 microns. (p. 386)

18, *19*, *23*—*Denso-sporites tenuis* Hoffmeister, Staplin and Malloy, n. sp.; *18*, holotype, size 43×47 microns; *19*, size 64×57 microns, ser. 18739; *23*, 44×45 microns, TCO-82, ser. 18641. (p. 387)

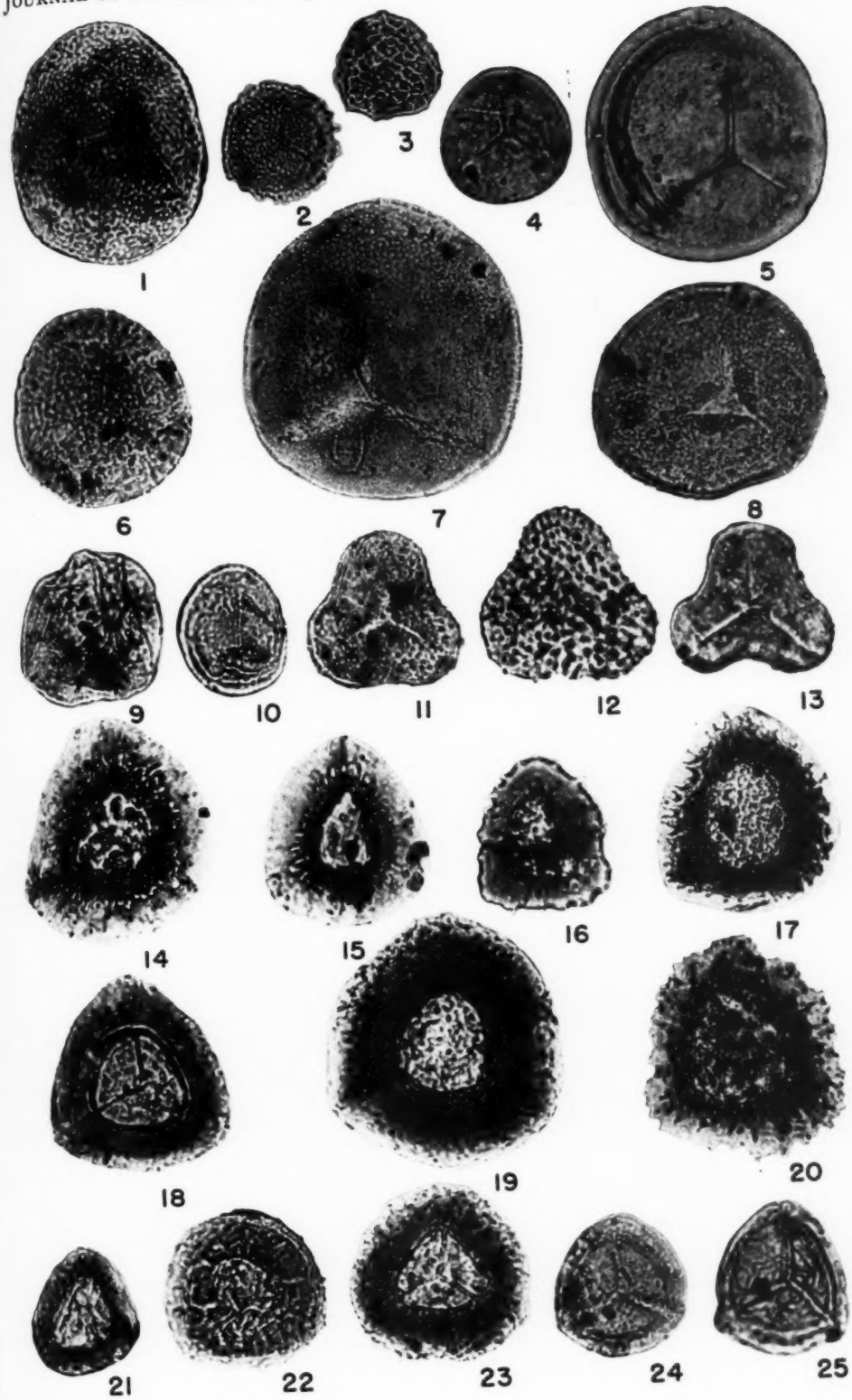
20—*Denso-sporites* type A; size 50×54 microns. (p. 387)

21—*Denso-sporites parvus* Hoffmeister, Staplin and Malloy, n. sp., holotype; size 32×34 microns. (p. 386)

22—*Denso-sporites brevispinosus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 38 microns. (p. 386)

24—*Cirratriradites uber* Hoffmeister, Staplin and Malloy, n. sp., holotype; 31.5×35 microns. (p. 383)

25—*Cirratriradites pseudoannulatus* (Kosanke, 1950), n. comb.; 31×37.5 microns, ser. 15940. (p. 383)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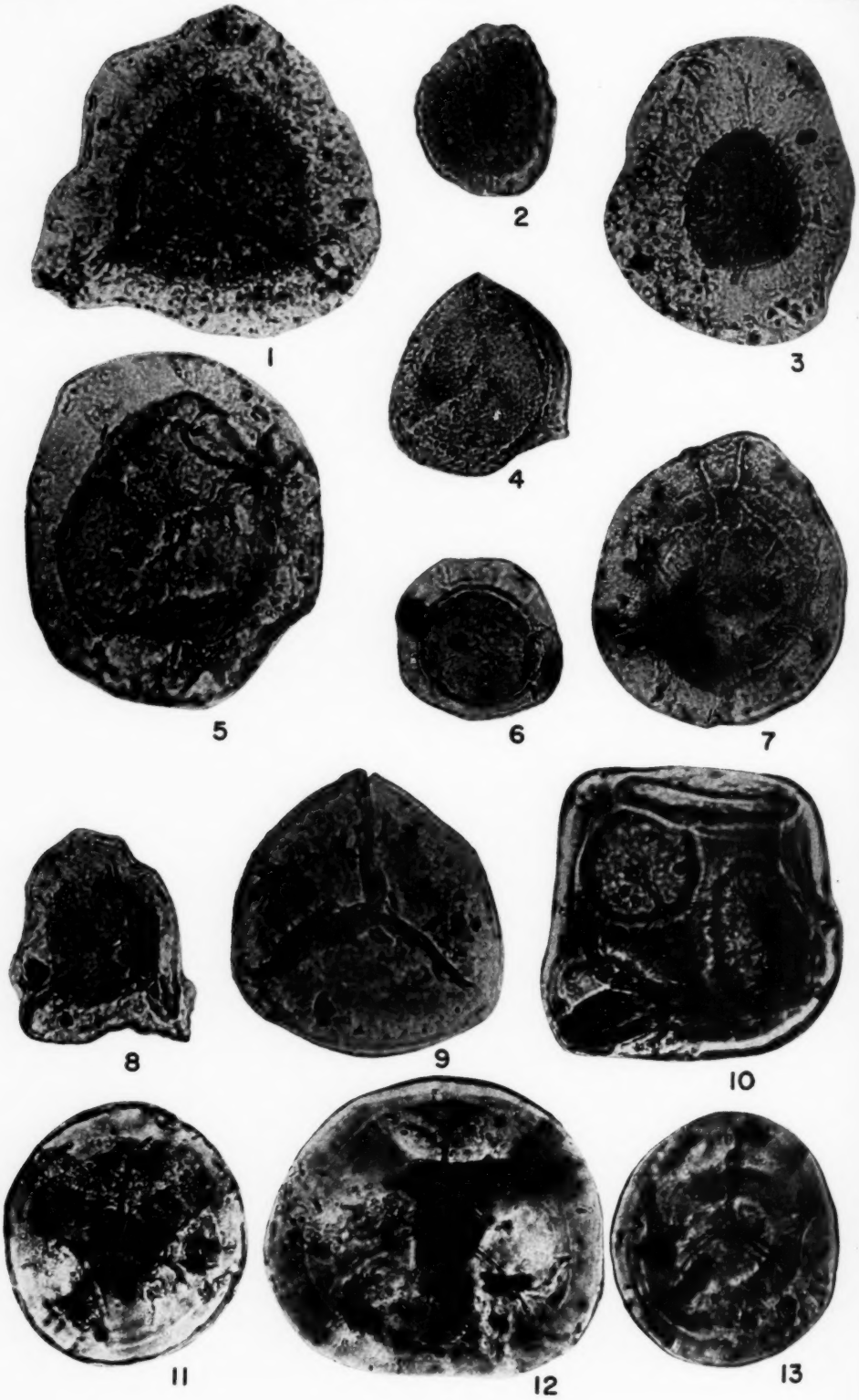
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TABLE 1—STATISTICAL ANALYSIS BY GENERA OF HARDINSBURG AND WALTERSBURG SAMPLES

Formation and locality	Sample number or depth (Total specimens counted in parentheses) M-marine; C-coal	*Cirratriradites*	*Punctatisporites*	*Densosporites*	*Granulatisporites*	*Schulzospora*	*Endosporites*	*Calamospora*	*Convolutispora*	Misc. Genera	Unknown (poor preservation)	Aletes
HARDINSBURG FORMATION												
Carter M. Tapp No. 3 (TCO-82)												
Webster County, Ky.	2071.5′ (300)	53	21	9	8	1	1	—	+	—	7	—
	2072′ (200)	48	26	8	6	1	—	—	—	1	10	—
	2075′ (200)	53	23	5	5	3	1	—	1	—	9	—
	2076′ (200)	41	30	6	6	1	3	+	—	—	13	—
	2077′ (200)	52	21	16	3	1	—	—	2	—	5	—
	2078′ (200)	48	31	12	4	1	+	—	+	—	4	—
	2079.4′ (200)	48	30	16	1	+	—	—	2	—	3	—
	2081′ (200)	46	35	6	6	+	1	+	1	—	5	—
	2081–84′(200)	46	36	8	3	—	1	—	—	—	6	—
	2085′ (200)	41	40	6	5	+	—	—	1	1	6	—
	2086′ (200)	50	36	4	4	—	2	+	+	+	4	—
	2087–88′(200)	42	36	5	4	1	+	—	—	—	12	—
Carter J. E. Horn No. 1 (TCO-153)												
Saline County, Ill.	No. 2 (200)	41	8	1	4	—	—	—	—	—	5	41[2]
	No. 1C (200)	88	1	4	2	—	—	2	—	2	1	—
	No. 3 (200)	39	7	2	4	—	+	1	1	4	6	36[2]
Outcrop Samples (TCO-143)												
Christian County, Ky.	No. 1M (200)	57	33	3	2	1	+	+	1	+	3	—
	No. 2M (200)	48	36	6	2	1	1	1	1	1	3	—
	No. 3M (200)	29	21	6	—	1	—	3	—	1	39	—
	No. 4M (200)	46	33	8	3	+	2	+	2	1	5	—
	No. 5M (200)	47	32	6	6	+	+	1	—	1	—	7
WALTERSBURG FORMATION												
Inland Pielemeier No. 3 (TCO-108)												
Gallatin County, Ill.	1993′–95′(400)	10	77[1]	—	1	10	—	1	—	1	—	—

[1] Small granulose usually alete forms, rarely with trilete rays of radius length; 65 percent.
[2] Small levigate sacs—cysts?

EXPLANATION OF PLATE 37

FIG. *1*—*Cirratriradites* type A; 61×75.6 microns. (p. 384)
2—*Cirratriradites granulatipunctatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 33.6×39.9 microns. (p. 382)
3—*Auroraspora solisortus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 61×67 microns. (p. 381)
4—*Cirratriradites praetergranulatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 44×48 microns. (p. 383)
5—*Endosporites endorugosus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 80×84 microns. (p. 387)
6—*Endosporites minutus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 40×42 microns. (p. 387)
7—*Endosporites pallidus* Schemel, 1950, TCO-82, ser. 19,317; 66×70 microns. (p. 388)
8—*Endosporites* type A; 35×49 microns. (p. 388)
9—Spore type A; 67 microns. (p. 397)
10—Spore type B; 80×86 microns. (p. 397)
11, 12—*Knoxisporites triradiatus* Hoffmeister, Staplin and Malloy, n. sp.; *11*, 59×65 microns, TCO-82, ser. 18,850; *12*, holotype, 80×86 microns. (p. 391)
13—*Knoxisporites rotatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 59×63 microns. (p. 390)

strata. *Convolutispora* n. gen. appears to reach its peak development in Chester time, although ranging from the Upper Devonian (Alberta, Canada, unpublished study) into the Pennsylvanian. *Schulzospora* and *Auroraspora* n. gen. are believed to be restricted in range from Upper Mississippian to Lower Pennsylvanian (Atokan) time. *Densosporites* is characteristic of Upper Mississippian and Lower Pennsylvanian rocks, and has not been found in the Lower Devonian or above the Des Moines series of the Pennsylvanian in the United States, although it has been recorded from the Permian rocks of U.S.S.R. (Luber, in Goubkin, 1938). *Rotaspora* is known only in Upper Mississippian rocks in the United States but has also been reported from the middle Senonian (Cretaceous) of Germany (Weyland and Krieger, 1953). *Knoxisporites* is present in Upper Mississippian and Lower Pennsylvanian rocks (Warrior Basin, Alabama, unpublished study).

Convolutispora and *Apiculati-sporites* seem to be more characteristic of Mississippian and Lower Pennsylvanian rocks than of beds of earlier or later Paleozoic age.

TAXONOMY

Several taxonomic systems have been applied to spores and pollen by various workers. Ibrahim (1933) and Loose (1932, 1934) erected form genera under which species were formally described using a binomial system. Their classification was completely artificial and based in large part on surface ornamentation. The difficulty of making a sharp valid separation of spore types as well as the inclusion of both megaspores and microspores in the same genus led to the early modification of this system by American and British workers. Schopf, Wilson, and Bentall (1944) enlarged and expanded this system with emendations and major revisions, basing some of their genera on the natural affinities of the spores as indicated by studies of fructifications. Kosanke (1950), Schemel (1950), and other American workers have followed this revised system. Raistrick and Simpson (1933) and Knox (1948) made use of a letter-numeral system under which type specimens were not selected and formal descriptions not made. Naumova (1937) and Luber and Waltz (1938) divided spores into five main form genera and described them under a binomial system. This classification proved too broad for practical application and has not been generally accepted by paleobotanists.

Knox (1938, 1939, 1950) made comprehensive studies of modern spores. Her investigations and those of others (Wilson, personal communication, 1954) showed that within a species of heterosporous plants the microspores may be trilete although the megaspores are monolete. Spore form (i.e. shape) may differ from species to species within the same genus. She concluded, therefore, that surface ornamentation is a more valid basis for classification than symmetry or form. *Plani-sporites*, *Spinososporites*, *Verrucoso-sporites* and *Microreticulati-sporites* were "suggested" as new form genera to include spores with smooth, spinose, verrucose and finely reticulate (mesh width less than 6 microns) or wrinkled exines respectively. These groups include within them spores of quite dissimilar aspect which can be separated into constant and distinct morphologic units. In common with many fossil groups, gradations in ornamentation are found among spore types which make separations on this basis alone extremely difficult. The obstacles to creating a "natural" classification of fossil spores and the dangers of such a system are brought out clearly by Knox's work and that of others before her.

Symmetry and form, however, offer practical bases for delineation of form genera. The authors do not believe that radial and bilateral spores of spherical, lenticular and tetrahedral form should be placed within the same form genus on the basis of ornamentation. This view agrees essentially with that held by modern German spore and pollen students (R. Potonie, Thomson, Kremp and others).

Important objections to the validity of the genera proposed by Knox (1950) can be raised on taxonomic grounds. *Punctati-sporites* and *Granulati-sporites* are discarded by her as being too broad in scope, and their genotypes assigned to a new genus, *Plani-sporites;* a procedure contrary to the International Code of Botanical Nomenclature (1952, p. 35, art. 62). The authors agree that *Punctati-sporites* (Ibrahim, 1933) Schopf, Wilson and Bentall, 1944, and other genera

are loosely defined groups, but as knowledge of spores increases they can be restricted readily to include their types and species having similar morphology. *Verrucososporites* Knox is erected for spores having features similar to those included in *Verrucosi-sporites* Ibrahim, 1933. *Spinoso-sporites* Knox in part duplicates *Apiculati-sporites* Ibrahim, 1933. Both genera, as defined by Knox, contain spores of different symmetry and form.

The genus *Microreticulati-sporites* as proposed by Knox comprised spores of both radial and bilateral symmetry. Potonie and Kremp emended it to include trilete forms with a reticulate surface having a mesh diameter of not more than 6 microns. The reticulations are somewhat variable in size on most spores of this general group and it seems impractical to separate at the generic level forms with a "Mesh 4–6 microns" (*M. maculatus* Knox) from forms with a "Mesh 5–8 microns" (*Reticulati-sporites facetus* Knox).

Knox proposed many new names at the specific level for the letter-number designations of Raistrick and Knox. As these lack citations of type specimens or localities (and may include forms where the type material is no longer available) they should not be recognized until they are properly validated under the International Code of Botanical Nomenclature.

Potonie and Kremp (1954) proposed many new genera and redefined others. Kremp (1954, personal communication) has prepared a manuscript covering all Paleozoic spore species which will be published in 1955. The classification used by Potonie and Kremp is "morphographic" and therefore is composed of true form genera. The present writers are in agreement with this goal. However, anticipating further revisions and additions to this system in the near future, the authors assign some species described in this paper to genera of Schopf, Wilson, and Bentall (1944) and not to the genera of Potonie and Kremp.

There is a vital need for clarification and redefinition of several of the present form genera of fossil spores, as well as a need for the universal adoption of a system of form classification, but the authors believe that this cannot be done without comprehensive consideration of the several systems now in the literature. Any system ultimately adopted should, however, be in accordance with the International Rules of Botanical Nomenclature. Such an undertaking is beyond the scope of this paper, and the authors, therefore, have adopted a conservative viewpoint, following for the most part the system employed by other American workers.

In the systematic descriptions which follow, three new genera, 37 new species, 10 unnamed specific types, five generically indeterminate spore types, and six new combinations are proposed (Table 2).

SYSTEMATIC PALEONTOLOGY

Genus ACANTHOTRILETES (Naumova, 1937) Potonie & Kremp, 1954

Description.—Spores radial, trilete; ornamentation ciliate, spines attenuate, often tubular, closely crowded, longer than twice their diameter; trilete often obscured by ornamentation.

Genotype.—*A. ciliatus* (Knox, 1950) Potonie and Kremp, 1954.

Remarks.—The tubular or ciliate nature of the spines distinguishes this genus from *Apiculati-sporites* and *Lophotriletes.*

ACANTHOTRILETES ECHINATUS Hoffmeister, Staplin & Malloy, n. sp.

Pl. 38, figs. 1–2

Description.—Spores radial, trilete; outline circular; ornamentation densely crowded thin tubular spines, tips narrowly rounded to blunt, sometimes hooked; trilete rays indistinct, simple, length approximately two-thirds spore radius; spore coat relatively thick, translucent; diameter 30–46 microns, spines 2–4.2 microns.

Holotype.—TCO–82, 2087–2088 ft., slide 2, ser. 19,473 (fig. 1), Hardinsburg formation; size 33.6×35.7 microns, spines 2–3.6 microns.

Remarks.—The densely crowded thin spines are characteristic of this species.

Occurrence.—Hardinsburg formation, TCO–82, TCO–153, TCO–143 localities 2 and 3; occasional.

Genus APICULATI-SPORITES (Ibrahim, 1933) Potonie & Kremp, 1954

Description.—Spores radial, trilete, circular; thickly covered with tapered cones whose basal diameter can equal their height,

TABLE 2—INDEX TO SPECIES OCCURRENCE

Species	Localities					
	TCO-82	TCO-153	TCO-143			
			1	2	3	4
Acanthotriletes echinatus	X	X		X	X	
Apiculati-sporites pineatus	?	X				
Auroraspora solisortus	X					
Calamospora cf. *C. straminea*	X					
C. type A	X	?				
Cirratriradites granulatipunctatus		X	X	X	X	
C. praetergranulatus	X					
C. pseudoannulatus	X					X
C. uber	X	X	X	X	X	X
Convolutispora ampla	X		X			
C. florida	X					
C. mellita	X					
C. tessellata	X					
C. venusta	X					X
C. type A		X				
Denso-sporites brevispinosus		X		?		X
D. capistratus	X					
D. parvus	X					X
D. spinifer	X	X				
D. tenuis	X	X	X	X	X	X
D. type A	X					
Endosporites endorugosus	X					
E. minutus	X					
E. pallidus	X		X			X
E. type A	X					
Grandispora spinosa	X					
Granulati-sporites cf. *G. pallidus*	X	X	X	X	X	X
G. politus	X					
G. tuberculatus	X					
Knoxisporites rotatus	X					
K. triradiatus	X					
Microreticulati-sporites fundatus		X				
Punctati-sporites? baccatus	X	X	X	X	X	X
P.? cerosus	X					
P. fissus	X	X	X	X		X
P. grandis	X					
P. pseudolevatus	X	X	X	X		
P. nitidus	X	X				X
P. plicatus	X	X	X			
P. reticulopunctatus		X				
P.? callosus	X					
P.? type A	X					
P.? type B	X					
P.? type C	X					
Raistrickia multipertica		X				
Reticulati-sporites decoratus	X					
R. type A	X					
R. type B	X					
Rotaspora fracta	X					
Schluzospora elongata	X		X			
S. cf. *S. rara*	X	X		X		X
Tripartites vetustus	X					X
Triquitrites marginatus	X					X
T. type A	X					
Spore type A	X					
Spore type B	X					
Spore type C	X					
Spore type D	X					
Spore type E	X					

more or less variable in size and shape, so closely crowded that their bases may touch; trilete often obscured by ornamentation.

Genotype.—*A. aculeatus* Ibrahim, 1933.

Remarks.—The large variable conical to palmate processes characterize this genus.

APICULATI-SPORITES PINEATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 38, fig. 3

Description.—Spores radial, trilete; outline circular, commonly compressed into an elliptical shape; ornamentation large overlapping crowded variable spatulate processes, basal dimension 6.7×2–8.4×3 microns, length 5–8 microns, tips variable, bluntly rounded to palmate and spinose; processes levigate; trilete rays simple, length approximately two-thirds spore radius, visible as faint lines on a few specimens; spore coat moderately thick, translucent; diameter 36–56 microns.

Holotype.—TCO-153, No. 1, slide 7, ser. 19,684, Hardinsburg formation; size 48.3×50.4 microns.

Remarks.—The processes may be seen in several views at the spore margin, some appearing as conical, or cylindrical spines.

Occurrence.—Hardinsburg formation, TCO-82 (?), TCO-153; occasional.

Genus AURORASPORA Hoffmeister, Staplin & Malloy, n. gen.

Description.—Spores radial, trilete; outline subcircular; central body subtriangular to subcircular in proximal view; bladder encloses spore body, width subequal, commonly folded because of extreme thinness, crenulate radially from the central body; central body smooth, granulose, or faintly reticulate; bladder delicate, transparent, levigate; trilete rays moderately well developed, lips raised into a narrow ridge extending to or almost to the margin of the central body; central body wall moderately thick, color dark amber yellow; bladder transparent and very thin, colorless.

Genotype.—*Auroraspora solisortus* Hoffmeister, Staplin, and Malloy, n. sp.

Remarks.—*Auroraspora* has a dark, subtriangular to subcircular central body and a delicate, transparent bladder. *Wilsonia* has a very indistinct central body and a comparatively heavy bladder. The central body of *Endosporites* approximates the bladder in thickness. Commonly the bladder has prominent folds which radiate from the central body. The affinities of these spore genera are cordaitalean in part, although Kosanke (personal communication, 1954) has found spores of *Endosporites* sp. definitely borne in cones of a lycopod. If the bladder is removed from *Auroraspora*, the possible lycopod affinity of the genus is suggested by the aspect of the central body. *Zonotriletes eurypteris* Waltz (in Luber and Waltz, 1938) from the Tournaisian (and Viséan?) of the U.S.S.R. perhaps belongs to *Auroraspora*.

AURORASPORA SOLISORTUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 37, fig. 3

Description.—Spores radial, trilete; proximal view subcircular to subtriangular; central body entirely (?) enclosed in thin transparent membrane; central body subtriangular to subcircular, bladder subcircular to weakly subtriangular; central body levigate, bladder finely granulose and without inner reticulation; trilete rays moderately well developed, lips slightly raised and without commissure, length almost equal to radius of central body; central body wall relatively thick, translucent, bladder transparent, extremely thin, and often finely folded; trilete sutures perhaps influence folding at the three radial corners, where folds are slightly thicker; size range 61–78 microns, bladder width beyond central body, 13–19 microns.

Holotype.—TCO-82, 2071 ft., slide 5, ser. 19,471, Hardinsburg formation; dimensions 61×67 microns, central body 21×32 microns, width of bladder beyond central body 14–19 microns.

Occurrence.—Hardinsburg formation, locality TCO-82; occasional.

Genus CALAMOSPORA Schopf, Wilson, & Bentall, 1944

Description.—Spores radial, trilete; outline circular to subcircular, originally spherical or subspherical; when compressed, characteristic sharp taper-point folds variously crescentic or narrowly lenticular in outline present; ornamentation characteristically levigate, occasionally minutely granulose or

rugose; trilete rays generally short, distinct, lip development moderate on some species, area contagionis often visible; spore coat thin in most species, but ranging between 1–15 microns, transparent to translucent, color light amber yellow to brown; diameter 30–165 microns.

Genotype.—*C. hartungiana* Schopf, in Schopf, Wilson, and Bentall, 1944.

Remarks.—Megaspores, microspores, and possibly isospores included within this genus are largely of calamarian origin.

CALAMOSPORA cf. C. STRAMINEA
Wilson & Kosanke, 1944
Pl. 38, fig. 16

Calamospora straminea WILSON & KOSANKE, 1944, Iowa Acad. Sci., vol. 51, p. 329, fig. 1.

Description.—Spores radial, trilete; original spherical shape indicated by arcuate compression folds; surface levigate; trilete rays distinct, simple, approximately two-thirds spore radius; area contagionis faintly visible; spore coat approximately 1 micron thick, transparent; diameter 35–48 microns.

Remarks.—*Calamospora straminea* Wilson and Kosanke, 1944, is reported to have a wall thickness of 3 microns, but is otherwise similar to the Hardinsburg forms.

Occurrence.—Hardinsburg formation, TCO-153, TCO-82; occasional.

CALAMOSPORA type A
Pl. 38, fig. 17

Description.—Spore radial, trilete; outline subcircular, spore coat compressed into sharp taper-point folds; spore surface levigate to finely granulose; trilete rays distinct, relatively long, approximately 31 microns, lacking distinct lips; spore coat approximately 1 micron thick, transparent; size 61×84 microns.

Remarks.—One specimen, TCO-82, 2077 ft., slide 3, ser. 15,670, Hardinsburg formation.

Genus CIRRATRIRADITES Wilson & Coe, 1940

Description.—Spores radial, trilete; shape lenticular; outline circular to subtriangular; equator marked by thin distinct flange of variable width and ornamentation, sometimes one or two concentric bands of thickening, often radially striate; central body smooth to rugose; central distal surface may have a ridge outlining an irregular area often divided into several sections; trilete rays often prominent, lips raised, sutures extend to edge of the spore body and usually continued as thickenings to edge of flange; size range 30–102 microns.

Genotype.—*C. maculatus* Wilson and Coe, 1940.

Remarks.—*Cirratriradites* includes forms with a distinct marginal flange which is thinner and often lighter in color than the central body. *Lycospora* has a narrow equatorial girdle on which thickened extensions of the trilete rays are not developed. A few species of *Denso-sporites* have well-developed triletes and resemble *Cirratriradites.* The following species and new combinations are placed in *Cirratriradites:*

1. *Cirratriradites minutus* Wilson and Coe, 1940, Amer. Mid. Nat., p. 183, pl. 1, figs. 11, 12.
   Lycospora minutus (Wilson and Coe) Schopf, Wilson, and Bentall, 1944, Illinois State Geol. Survey, Rept. Invest. no. 91, p. 54.
   Lycospora minutus (Wilson and Coe) Schopf, Wilson, and Bentall, in Knox, 1950, Trans. Proc. Bot. Soc. Edinburgh, vol. 35, part 3, p. 328, fig. 275.
2. *Cirratriradites pseudoannulatus* (Kosanke) n. comb.
   Lycospora pseudoannulata Kosanke, 1950, Illinois State Geol. Survey, Bull. 74, p. 45, pl. 10, fig. 7.
3. *Cirratriradites punctatus* (Kosanke) n. comb.
   Lycospora punctata Kosanke, 1950, idem., p. 45, pl. 10, fig. 3.

L. R. Wilson concurs with the authors in the restoration of *C. minutus.* The genotype of *Lycospora* Wilson and Coe, 1940, *L. micropapillatus,* does not possess extensions of the lips onto the girdle as shown in the original illustration by Wilson and Coe (L. R. Wilson, personal communication, 1954, and cotypes examined by the authors). The genotype of *Cirratriradites, C. maculatus,* has been placed by Potonie and Kremp in synonomy with *C. saturni* (Ibrahim) Schopf, Wilson, and Bentall, 1944. It is not certain that these are the same species.

CIRRATRIRADITES GRANULATIPUNCTATUS
Hoffmeister, Staplin & Malloy, n. sp.
Pl. 37, fig. 2

Description.—Spores radial, trilete; outline subcircular; equatorial flange narrow; ornamentation, central body granulose-

punctate, flange finely but irregularly striate; trilete rays distinct, lips slightly raised, weak on some specimens, extending to outer margin of spore body and rarely into flange; spore body coat translucent, flange transparent and thinner than central body wall; size range 35–52 microns, flange 2.5–5.0 microns.

Holotype.—TCO-108, 1993–95 ft., slide 7, ser. 19,623, Waltersburg formation, Chester series; dimensions 33.6×39.9 microns, flange 3–5 microns.

Remarks.—The characteristic subcircular shape, relatively thick spore body wall, less well marked trilete suture and lack of arcuate compression folds between central body and flange distinguish this species from *C. uber*. Specimens of this form are rare and poorly preserved in the Hardinsburg samples but are abundant in the Waltersburg sample.

Occurrence.—Hardinsburg formation, TCO-153; TCO-143, localities 1, 2, and 3; Waltersburg formation, TCO-108.

CIRRATRIRADITES PRAETERGRANULATUS
Hoffmeister, Staplin & Malloy, n. sp.
Pl. 37, fig. 4

Description.—Spores radial, trilete; shape lenticular, proximal outline subtriangular; equator marked by a moderately wide flange; central body outline indistinct; surface of both central body and flange equally granulose; trilete rays distinct, lips moderately developed, extending to outer flange margin as thickenings; spore coat thin, translucent to transparent; size range 43–48 microns, flange 3.7–6 microns.

Holotype.—TCO-82, 2071 ft., slide 10, ser. 18,821, Hardinsburg formation; dimensions, 44×48 microns, flange 5.6 microns.

Remarks.—The granulose surface of both spore body and flange, serving to obscure the central body outline, characterizes this species.

Occurrence.—Hardinsburg formation, locality TCO-82; occasional.

CIRRATRIRADITES PSEUDOANNULATUS
(Kosanke)
Pl. 36, fig. 25

Lycospora pseudoannulata KOSANKE, 1950, Illinois State Geol. Survey, Bull. 74, p. 45, pl. 10, fig. 7.

Description.—Spores radial, trilete; outline subtriangular; equatorial flange narrow but well developed as an appendage to the spore body, width may be exaggerated by arcuate folding between the spore body and flange; ornamentation, spore body finely granulose to nearly smooth, flange levigate, often appearing ragged or perforate because of maceration; trilete rays distinct, lips raised and slightly extended as thickenings onto the flange; spore coat thin, translucent to transparent; size range 30–42 microns, flange 3–6 microns.

Remarks.—The presence of a distinct flange on the forms observed in the Hardinsburg formation, as well as on the specimens assigned by Kosanke (1950) to *Lycospora pseudoannulata*, justifies the transfer of this species to *Cirratriradites*.

Occurrence.—Hardinsburg formation, localities TCO-82, TCO-143 No. 5; common.

CIRRATRIRADITES UBER Hoffmeister,
Staplin & Malloy, n. sp.
Pl. 36, fig. 24

Description.—Spores radial, trilete; shape lenticular; outline subtriangular to subcircular; equatorial flange narrow, width often exaggerated by prominent arcuate peripheral folding on the central body; ornamentation, central body finely but distinctly granular, flange smooth or faintly striate; trilete rays strong, lips prominent, raised, extended into flange as thickenings; spore coat thin, translucent to transparent, flange often appears perforate or ragged because of maceration; diameter 28–42 microns, flange 1.5–5 microns.

Holotype.—TCO-82, 2072 ft., slide 3, ser. 18,608, Hardinsburg formation; diameter, 31.5×35 microns, flange 3.8–5 microns.

Remarks.—This species, the most abundant spore in the Hardinsburg formation, also constitutes a large part of the spore florules of Lower Pennsylvanian (Pottsville) coals of the Warrior Basin, Alabama (unpublished study by the authors). The distinctly granulose central body distinguishes this species from *C. pseudoannulatus* (Kosanke).

Occurrence.—Hardinsburg formation, localities TCO-82, TCO-153, TCO-143 No. 1–5; abundant. Waltersburg formation, locality TCO-108, abundant. Pottsville series, Warrior Basin, Alabama; abundant.

CIRRATRIRADITES type A
Pl. 37, fig. 1

Description.—Spore radial, trilete; shape lenticular; outline subtriangular; equatorial flange broad; overall size 61×75.6 microns, central body 47.6×50.4 microns; central body and flange irregularly punctate; central body thick in comparison to flange; short radially arranged processes present where the flange joins central body; trilete rays strong, lips raised, extended to flange margin as thickenings; spore translucent to transparent.

Remarks.—One specimen, TCO-82, 2078 ft., slide 1, ser. 15,754, Hardinsburg formation.

Genus CONVOLUTISPORA Hoffmeister, Staplin & Malloy, n. gen.

Description.—Spores radial, trilete; circular to subcircular, probable original spherical shape indicated by lack of orientation preference; ornamentation closely packed overlapping anastomosing vermiculate or obervermiculate ridge-like processes, often causing a convoluted or coarsely reticulate-punctate appearance; trilete rays short, usually simple, but may have distinct lips, often obscured by the overlapping ridges; spore coat thick, lacking conspicuous folding, translucent; diameter 40–150 microns.

Genotype.—*Convolutispora florida* Hoffmeister, Staplin, and Malloy, n. sp.

Remarks.—The closely packed anastomosing ridges distinguish this genus. *Cristatisporites* Potonie and Kremp, 1954, includes forms in which large processes are connected at their bases to form serrate ridges which are not anastomosing. Described species referred to the genus include:

1. *Convolutispora tuberculata* (Waltz) n. comb.
   Azonotriletes tuberculatus, Waltz, 1938, in Luber and Waltz, Trans. Cent. Geol. and Prospecting Inst., Fasc. 105, p. 12, pl. 1, fig. 12, pl. A, fig. 6.
2. *Convolutispora* (?) *variotuberculata* (Luber) n. comb.
   Azonotriletes variotuberculatus, Luber, 1938, in Luber and Waltz, idem., p. 24, pl. 5, fig. 67.

CONVOLUTISPORA AMPLA Hoffmeister, Staplin & Malloy, n. sp.
Pl. 38, fig. 12

Description.—Spores radial, trilete; originally spherical; outline circular to subcircular, folding may be present; ornamentation crowded vermiculate anastomosing ridges, depressed areas vary from small lacunae to irregularly radiating depressions; trilete sutures obscure, sometimes visible as simple grooves crossing the ridges, length approximately two-thirds spore radius; spore coat relatively thick, short thick arcuate compression folds sometimes present, translucent; diameter 40–75 microns; ridges 1–2.8 microns wide, 1–2.8 microns high.

Holotype.—TCO-143 No. 5, slide 3, ser. 19,280, Hardinsburg formation; 62×64 microns.

Remarks.—This species is characterized by crowded ridges, and depressions which vary from small and subcircular to irregularly radiate ("crow foot"). The ridges are narrower than in other species described in this paper.

Occurrence.—Hardinsburg formation, localities TCO-82, TCO-143 No. 1, 5; occasional.

CONVOLUTISPORA FLORIDA Hoffmeister, Staplin & Malloy, n. sp.
Pl. 38, figs. 5, 6

Description.—Spores radial, trilete; proximal outline circular to subcircular; ornamentation closely packed coarse obervermiculate convoluted ridges, often flattened by compression; trilete rays slightly exceed one-half spore radius, usually obscured, lips raised; spore coat relatively thick, translucent; diameter 39–50 microns, ridges 2.8–6.3 microns wide.

Holotype.—TCO-82, 2086 ft., slide 1, ser. 16,551 (Pl. 38, fig. 6), Hardinsburg formation; diameter 49 microns, ridges 2.8–5.6 microns wide.

Remarks.—The coarse broad ridges of this otherwise relatively small form distinguish it from allied species.

Occurrence.—Hardinsburg formation; locality TCO-82; rare.

CONVOLUTISPORA MELLITA Hoffmeister, Staplin & Malloy, n. sp.
Pl. 38, fig. 10

Description.—Spores radial, trilete; outline circular, folding generally absent; surface strongly convolute with broad anastomosing ridges, producing a roughly reticulate appearance; trilete rays obscure, but

may be detected as faint lines by varying plane of focus; length slightly over one-half spore radius; spore coat relatively thick, translucent; diameter 60–85 microns, width of ridges 2.8–5.6 microns.

Holotype.—TCO-82, 2072 ft., slide 2, ser. 18,595, Hardinsburg formation; size 82×84 microns.

Remarks.—Large size, thickly convolute surface, and roughly reticulate appearance characterize this species.

Occurrence.—Hardinsburg formation; locality TCO-82; occasional.

CONVOLUTISPORA TESSELLATA Hoffmeister, Staplin & Malloy, n. sp.
Pl. 38, fig. 9

Description.—Spores radial, trilete; originally spherical; outline circular to subcircular, conspicuous folding lacking; ornamentation thick, irregular, partly anastomosing, broad ridges of variable width and height, narrow to rounded in profile; trilete suture present but obscured by ornamentation; spore coat relatively thick, translucent; diameter 45–86 microns, ridges 2.8–6.5 microns wide, 2–5.6 microns high.

Holotype.—TCO-82, 2087–2088 ft., slide 1, ser. 16,527, Hardinsburg formation; diameter 86 microns.

Occurrence.—Hardinsburg formation; locality TCO-82; occasional.

CONVOLUTISPORA VENUSTA Hoffmeister, Staplin & Malloy, n. sp.
Pl. 38. fig. 11

Description.—Spores radial, trilete; originally spherical; outline circular to subcircular, conspicuous folding lacking; ornamentation coarse, irregularly developed arête-like ridges, anastomose in part; trilete sutures simple grooves intersecting the ornamentation, length approximately two-thirds spore radius; spore coat relatively thick, translucent; diameter 44–66 microns; ridges 2.8–5.6 microns wide, 1–3 microns high.

Holotype.—TCO-82, 2072 ft., slide 5, ser. 15,814, Hardinsburg formation; diameter 61.6 microns, trilete rays 16–22.4 microns.

Remarks.—The crowded arête-like ridges, variable in height, characterize this species.

Occurrence.—Hardinsburg formation; localities TCO-82 and TCO-143 No. 5; rare.

CONVOLUTISPORA type A
Pl. 38, fig. 7

Description.—Spores radial, trilete; outline circular to subcircular; no preferred orientation or conspicuous folding; surface coarsely vermiculate, ridges irregularly arranged, variable in height, often lobate, width 1.5–5.6 microns, height 1–2.9 microns; trilete simple, distinct, approximately one-half spore radius; spore coat relatively thick, translucent; diameter 38–45 microns.

Remarks.—Specimens are too rare and poorly preserved to justify the erection of a new species.

Occurrence.—Hardinsburg formation; localities TCO-82, TCO-153 No. 1 (coal); rare.

Genus DENSO-SPORITES (Berry) Schopf, Wilson & Bentall, 1944

Description.—Spores radial, trilete; proximal view circular to subtriangular; equatorial region thickened, width variable, may consist of one or two variable concentric zones of thickening, rods, ridges, spines, plates often present, entire region sometimes tapering to thin translucent marginal area; surface levigate to apiculate and rugose; margins smooth to serrate; trilete rays indistinct to prominent, lips simple or raised, rarely extending into the equatorial region; spore coat translucent, color dark brown to light amber yellow; size 27–100 microns.

Genotype.—*D. covensis* Berry, 1937.

Remarks.—*Denso-sporites* (Berry) Schopf, Wilson, and Bentall, 1944, is characterized by possessing a thick, subopaque to translucent equatorial margin surrounding a thin-walled translucent to transparent central area. The marginal area may be simple or divided into zones of different structure and thickness. Transitions from simple to zonate margins are possible within a single species (see *Denso-sporites brevispinosus*). The authors therefore believe that division of *Denso-sporites* (Berry) Schopf, Wilson and Bentall, 1944, into simple (*Anulati-sporites*) and complex (*Denso-sporites*) forms as proposed by Potonie and Kremp (1954) is not valid on the generic level. *Denso-sporites* (Berry) Schopf, Wilson, and Bentall, 1944, should not be confused with circular forms similar to *Simozonotriletes* (Naumova, 1937)

in which the equatorial region is not dark and is not attached in the form of a gable.

DENSO-SPORITES BREVISPINOSUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 22

Description.—Spores radial, trilete; outline subcircular; equatorial region variable, may appear to have two sharply demarked zones, inner region thick, outer thin and translucent, but entire equatorial region occasionally transitional and tapering; ornamentation, minute widely scattered spines on equatorial region, central body granular, often somewhat folded; trilete sutures, when present, appear as narrow ridges extending slightly into the equatorial region; diameter 34–40 microns.

Holotype.—TCO-153, No. 1, 2325 ft. (coal), slide 9 ser. 19,694, Hardinsburg formation; diameter 38 microns, equatorial region 11–12 microns.

Remarks.—This species is characterized by its subcircular shape and minutely spinose equatorial region.

Occurrence.—Hardinsburg formation; localities TCO-153, TCO-143 No. 2 (?), 5; occasional.

DENSO-SPORITES CAPISTRATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, figs. 14, 15

Description.—Spores radial, trilete; outline convexly subtriangular; thickened equatorial region divided into three zones, inner zone thick, middle zone variable in thickness, composed of radiating crowded variable rods or cylindrical processes, outer zone thin and translucent, tapering to an even outer margin; central body granulose; widely scattered minute conical spines sometimes present on outer zone; trilete rays, when preserved, appear as narrow ridges extending to the inner edge of equatorial region; size range 41–61 microns.

Holotype.—TCO-82, 2072 ft., slide 8, ser. 18,650 (Pl. 36, fig. 15), Hardinsburg formation; dimensions 41×46 microns, inner zone 2.5 microns, middle zone 2.5–3 microns.

Remarks.—The prominent middle equatorial zone bearing well-developed rods characterizes the species. *Zonotriletes variabilis* Waltz, 1938, a Russian form, may be similar to *D. capistratus*.

Occurrence.—Hardinsburg formation, locality TCO-82; rare.

DENSO-SPORITES PARVUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 21

Description.—Spores radial, trilete; outline subcircular; equatorial region divided into two zones, inner zone thick, irregularly scalloped at outer edge, outer zone thin, translucent; ornamentation, central body granulose, equatorial region levigate to finely granulose; spore margin smooth; trilete suture not observed; diameter 28–36 microns.

Holotype.—TCO-82, 2087–2088 ft., slide 5, ser. 18,842, Hardinsburg formation; dimensions 32×34 microns, equatorial region 6.3 microns.

Remarks.—Some specimens show only a single zone of equatorial thickening. In common with many species of *Densosporites* there is much variation. *D. reynoldsburgensis* Kosanke, 1950, is larger, has well-defined folds surrounding the central body, and is more minutely granulose.

Occurrence.—Hardinsburg formation, localities TCO-82 and TCO-143 No. 5; occasional.

DENSO-SPORITES SPINIFER Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, figs. 16, 17

Description.—Spores radial, trilete; outline convexly subtriangular; equatorial region of nearly equal thickness throughout its width, only slightly thinner at outer margin, almost opaque; ornamentation, central body coarsely granulose, spines of equatorial region scattered to crowded, 2–6 microns long, sometimes divided, extremely variable in shape and disposition; outer margin spinose; trilete sutures, when preserved, extend slightly into the thickened equatorial region; diameter 32–48 microns.

Holotype.—TCO-82, 2075 ft., slide 3, ser. 19,066 (Pl. 36, fig. 17); Hardinsburg formation; dimensions 42×46 microns, equatorial region approximately 10 microns.

Remarks.—The almost opaque and strongly spinose equatorial region characterize this species. The Russian species *Zonotriletes dentatus* Waltz, 1938, is larger, but

cannot be directly compared with *D. spinifer*, n. sp.

Occurrence.—Hardinsburg formation; localities TCO-82, TCO-153; occasional.

DENSO-SPORITES TENUIS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, figs. 18, 19, 23

Description.—Spores radial, trilete; outline convexly subtriangular; equatorial region almost opaque near central body, tapering to an even, thin translucent outer marginal area; ornamentation scattered minute granulations on the central body, usually absent in equatorial area, always more prominent on the central body; trilete often prominent, lips often preserved as narrow thickened ridges extending slightly into the equatorial region; diameter 38–63 microns, equatorial region 12–19 microns.

Holotype.—TCO-82, 2078 ft., slide 2, ser. 15,775, (Pl. 36, fig. 18), Hardinsburg formation; dimensions 43×47 microns, central body 26 microns, equatorial region 12 microns.

Remarks.—The commonly preserved trilete rays and evenly tapered equatorial region characterize this species and distinguish it from *Denso-sporites sphaerotriangularis* Kosanke, 1950.

Occurrence.—Hardinsburg formation; localities TCO-82, TCO-153, TCO-143 No. 1, 2, 3, 5; abundant.

DENSO-SPORITES type A
Pl. 36, fig. 20

Description.—Spore radial, trilete; outline subtriangular; equatorial thickened region thins rapidly to a translucent outer area; ornamentation small scattered conical spines, length 1–3 microns, diameter at base 1–2 microns, separation 4–6 microns, much smaller on central body; outer margin serrate; trilete suture not visible on the single specimen; dimensions 50×54 microns, equatorial region 10–12 microns.

Remarks.—TCO-82, 2071 ft., slide 1, ser. 15,928, Hardinsburg formation; one specimen.

Genus ENDOSPORITES Wilson & Coe, 1940

Description.—Spores radial, trilete; proximal outline circular to subcircular; central body circular to subtriangular, enclosed in a bladder-like membrane; bladder commonly folded, folds often radiating from central body; ornamentation, central body granulose, levigate or punctate, bladder exterior punctate, granulose or legivate, interior sometimes faintly reticulate; trilete rays extremely variable in development, sometimes reflected as folding into the bladder; bladder wall thinner than central body wall. Size range 50–175 microns.

Genotype.—*E. ornatus* Wilson and Coe, 1940.

Remarks.—The diagrammatic sketches of *Endosporites* in Schopf, Wilson and Bentall (1944, pl. 2, fig. 14a–c) are in error, for the bladder should be shown as completely enclosing the central body. Comparisons of *Auroraspora*, *Endosporites*, and *Wilsonia* are made in the remarks following the description of *Auroraspora*, n. gen.

ENDOSPORITES ENDORUGOSUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 37, fig. 5

Description.—Spores radial, trilete; proximal view circular to subcircular; central body enclosed by a bladder; bladder commonly faintly folded, folds radial from the central body; ornamentation, spore body and bladder surfaces smooth to weakly granulose; trilete rays, when visible, two-thirds central body radius, reflected as folds on the bladder; periphery of central body thickened by folding; central body spore coat moderately thick but transparent, bladder relatively thin, transparent; size range 53–84 microns, central body 40–58 microns.

Holotype.—TCO-82, 2072 ft., slide 5, ser. 15,811, Hardinsburg formation; size 84×80 microns, central body 50×59 microns.

Remarks.—The wider bladder, a larger overall size by 14 microns, and the folded central body periphery distinguish this species from *E. pallidus* Schemel, 1950.

Occurrence.—Hardinsburg formation, TCO-82; occasional.

ENDOSPORITES MINUTUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 37, fig. 6

Description.—Spores radial, trilete; outline circular to subcircular; central body enclosed by a bladder; bladder often slightly folded, folds arranged radially from the cen-

tral body; ornamentation central body surface faintly granulose; trilete rays weak, simple, approximately two-thirds central body radius; central body coat relatively thick, translucent, bladder thin, transparent; size range 40–45 microns, central body 25–30 microns.

Holotype.—TCO-82, 2075 ft., slide 6, ser. 19,077, Hardinsburg formation; size 42×40 microns, central body 25–30 microns.

Remarks.—This species differes from *E. pallidus* Schemel, by possessing a strongly outlined central body with a well developed trilete suture, and also by its much smaller size.

Occurrence.—Hardinsburg formation, TCO-82; rare.

ENDOSPORITES PALLIDUS Schemel, 1950
Pl. 37, fig. 7

Endosporites pallidus SCHEMEL, 1950, Jour. Paleontology, vol. 24, no. 2, pp. 239–240, pl. 40, fig. 3.

Remarks.—The total diameter is 53–80 microns, as compared with 54–66 microns for specimens from a Lower Carboniferous coal of Utah studied by Schemel.

Occurrence.—Hardinsburg formation; TCO-82; TCO-143 localities 1 and 5; common.

ENDOSPORITES type A
Pl. 37, fig. 8

Description.—Spore radial, trilete; proximal outline subcircular; spore body enclosed by a bladder; bladder folded, folds arranged radially from the central body; spore body surface granulose, bladder levigate to faintly granulose; trilete rays not observed; central body coat relatively thick, translucent, bladder extremely thin, transparent; size 35×49 microns, central body 24×27 microns, bladder 9.5 microns.

Remarks.—One specimen, TCO-82, 2075 ft., slide 10, ser. 19,104, Hardinsburg formation.

Genus GRANDISPORA n. gen.
Text-fig. 3

Description.—Spores radial, trilete; central body enclosed by a bladder, both subcircular; central body levigate (?); possibly punctate or granulose; bladder wall punctate to granulose, possibly levigate, with

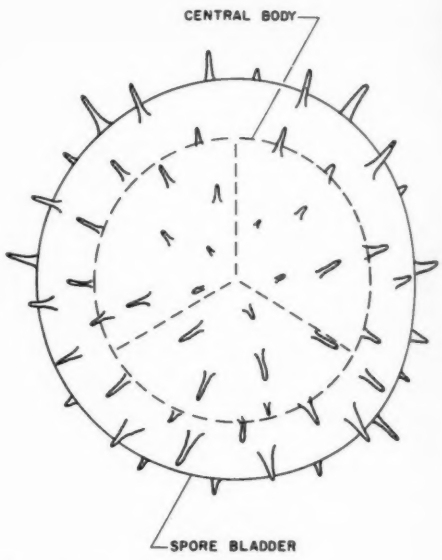


FIG. 3—*Grandispora* Hoffmeister, Staplin and Malloy, n. gen. Diagrammatic proximal view of spore.

prominent scattered spines; trilete rays weak, simple, apparently extend to edge of central body; central body wall only slightly thicker than the bladder wall, translucent.

Genotype.—*Grandispora spinosa* Hoffmeister, Staplin and Malloy, n. sp.

Remarks.—The spinose bladder distinguishes this genus from *Endosporites*. *Grandispora* appears to be rare in the Hardinsburg formation.

GRANDISPORA SPINOSA Hoffmeister, Staplin & Malloy, n. sp.
Pl. 39, figs. 10, 14

Description.—Spores radial, trilete; proximal view of both central body and bladder circular to subcircular; both bladder and central body punctate to slightly granulose; bladder of equal width around the central body, spinose, processes 2–8 microns long and 8–25 microns apart; trilete indistinct, simple, perhaps extends to edge of central body; dimensions 100–143 microns, central body 84–100 microns.

Holotype.—TCO-82, 2077 ft., slide 6, ser. 19,311 (Pl. 39, fig. 10), Hardinsburg formation; diameter 118 microns, central body 84×95 microns.

Remarks.—This species is the only form

assignable to *Grandispora* observed in the samples studied.

Occurrence. — Hardinsburg formation, TCO-82; rare.

Genus GRANULATI-SPORITES (Ibrahim) Schopf, Wilson, and Bentall, 1944

Description.—Spores radial, trilete; proximal view concavely triangular to convexly subtriangular; original lenticular shape indicated by proximal-distal orientation of most specimens; interradial regions concave to convex; ornamentation various; trilete sutures usually long, length two-thirds or more of spore radius, commissure frequently distinct, lips usually indistinct; spore coat exhibits little overall variation in thickness; translucent; size range 25–75 microns.

Genotype.—*G. granulatus* Ibrahim, 1933.

Remarks.—Potonie and Kremp (1954) include only granulose forms in *Granulati-sporites* Ibrahim.

GRANULATI-SPORITES cf. G. PALLIDUS Kosanke, 1950
Pl. 36, fig. 11

Granulati-sporites pallidus KOSANKE, 1950, Illinois State Geol. Survey, Bull. 74, pp. 21–22, pl. 3, fig. 3.

Description.—Spores radial, trilete; proximal outline subtriangular, interradial margins concave, radial margins rounded; original lenticular shape indicated by preferred proximal-distal orientation; surface rugose to papillate; trilete suture one-half to two-thirds spore radius, rays distinct, tending to gape; spore coat translucent to transparent; size range 23–42 microns.

Remarks.—The sequence of observed specimens grades into both *G. pallidus* and *G. granularis* Kosanke, 1950. The ornamentation of most specimens, however, resembles that of *G. pallidus*. The species is common in all the Hardinsburg samples.

GRANULATI-SPORITES POLITUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 13

Description.—Spores radial, trilete; proximal outline subtriangular, interradial margins concave or slightly convex, radial margins rounded; original lenticular shape indicated by preferred proximal-distal orientation; surface smooth to infra-punctate; trilete suture broad, two-thirds to three-fourths spore radius; spore coat moderately thin, transparent to translucent; size range 26–38 microns.

Holotype.—TCO-82, 2077 ft., slide 6, ser. 15,718, Hardinsburg formation; 37.5 microns.

Remarks.—This species differs from *Granulati-sporites* cf. *G. pallidus* and *G. tuberculatus* in having a smooth spore coat. This species would be assigned to *Leiotrilites* (Naumova, 1937) in the classification of Potonie and Kremp (1954).

Occurrence. — Hardinsburg formation, TCO-82; occasional.

GRANULATI-SPORITES TUBERCULATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 12

Description.—Spores radial, trilete; proximal outline subtriangular, interradial areas concave, radial margins rounded; original lenticular shape indicated by preferred proximal-distal orientation; surface tuberculate to spinose; trilete suture often obscure, extending three-fourths spore radius; spore coat moderately thick; size range 37.5–41.5 microns.

Holotype.—TCO-82, 2086 ft., slide 6, serial 1,6556, Hardinsburg formation; 41.5 microns.

Remarks.—The heavy conical tuberculae distinguish this species from *Granulati-sporites politus*, *G.* cf. *G. pallidus*, and others of this genus. *G. microsaetosus* (Loose) Schopf, Wilson and Bentall, 1944, possesses thinner, more acutely pointed processes.

Occurrence. — Hardinsburg formation, TCO-82; occasional.

Genus KNOXISPORITES Potonie & Kremp, 1954
Text-fig. 4.

Description.—Spores radial, trilete; outline circular to subcircular; arcuate compression folds occasional; equatorial girdle present, three extensions from the girdle reach to or slightly enclose the ends of the trilete rays; distal surface often marked by a circular ring connected to the girdle by three extensions rotated 60 degrees from those of the trilete rays; circular ring sometimes absent and the three extensions joined at the distal pole; ornamentation various;

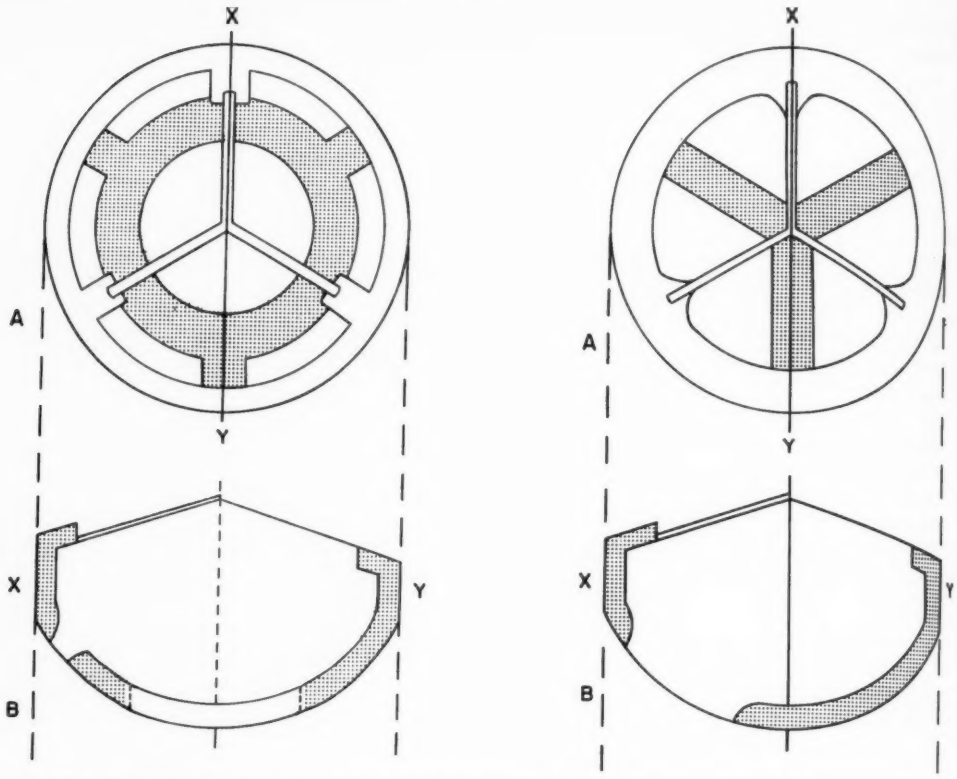


FIG. 4—Forms of *Knoxisporites* with and without distal ring of thickening. A. Proximal view. B. Polar section along the plane XY.

trilete rays prominent, lips raised, length approximately three-fourths spore radius; spore coat translucent to transparent, color amber brown; girdle, distal ring, and extensions connecting trilete rays and distal ring to girdle thicker than remainder of spore coat.

Genotype.—*Knoxisporites hageni* Potonie and Kremp, 1954.

Remarks.—The thickenings at the ends of the trilete rays may be similar to those of *Cadiospora* Kosanke, 1950. *Knoxisporites* is also present in Lower Pennsylvanian rocks of Alabama (unpublished study) and Namurian and Westphalian rocks of Europe and Asia. The botanical affinities are unknown.

KNOXISPORITES ROTATUS Hoffmeister, Staplin & Malloy., n. sp.
Pl. 37, fig. 13

Description.—Spores radial, trilete; outline circular; arcuate compression folds common; equatorial girdle present, three extensions of which attach to and enclose the ends of the trilete rays; a circular ring of thickening on distal surface, joined to girdle by three extensions rotated 60 degrees from the position of the trilete rays; spore coat levigate; trilete rays distinct, lips strongly raised, length two-thirds to three-fourths spore radius; spore coat transparent, color light amber brown; diameter 52–65 microns.

Holotype.—TCO-82, 2081 ft., slide 5, ser. 18,672 Hardinsburg formation; dimensions, width of distal circular band 7.3 microns, diameter of area enclosed by band, 24 microns, width of extensions, approximately 5 microns.

Remarks.—The extensions of the girdle which are attached to both the trilete tips and the distal ring are often indistinct.

Occurrence.—Hardinsburg formation, locality TCO-82; occasional.

KNOXISPORITES TRIRADIATUS Hoffmeister, Staplin & Malloy, n. sp.
Plate 37, figs. 11, 12

Description.—Spores radial, trilete; outline circular, sometimes folded into a roughly rectangular shape; arcuate compression folds indicate a probable subspherical form; orientation usually proximal-distal; proximal surface smooth; equatorial thickening or girdle broad, with three acute inward projections at the radial positions which extend to or slightly beyond the ends of the trilete rays; distal surface smooth, three bands of thickening radiate from the pole to join the equatorial girdle, and are rotated 60 degrees from the trilete mark of the proximal surface; trilete rays distinct, lips moderate, length two-thirds spore radius; spore coat sub-transparent, color amber brown; diameter 50–88 microns.

Holotype.—TCO-82, 2087 ft., slide 6, ser. 18,939 (Pl. 37, fig. 12), Hardinsburg formation; size 80×86 microns, girdle 10 microns, distal bands 12 microns.

Remarks.—Differentiation in the ornamentation of the central body and girdle has been noted in Lower Pennsylvanian (Pottsville) species of Alabama (unpublished study).

Occurrence.—Hardinsburg formation, locality TCO-82; occasional.

Genus MICRORETICULATI-SPORITES (Knox) Potonie & Kremp, 1954

Description.—Spores trilete, subtriangular to circular, exine extrareticulate with small lumina which rarely exceed 6 microns in diameter, muri imperfect, variable in height.

Genotype.—*Microreticulati-sporites lacunosus* (Ibrahim) Knox, 1950.

MICRORETICULATI-SPORITES FUNDATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 3

Description.—Spores radial, trilete; outline circular to subcircular; surface distinctly reticulate; ridges 0.6 microns wide and up to one micron high, lacunae variously shaped, 1–3 microns diameter; trilete indistinct on most specimens; spore coat a single layer, translucent, variable in thickness because of reticulum; diameter 20–29 microns.

Holotype.—TCO-153, No. 3, slide 8, ser. 19,396, Hardinsburg formation; 27×29 microns.

Remarks.—The small diameter and distinctly reticulated surface of the spore are characteristic. The lacunae and ridges are finer than in *Microreticulati-sporites spicatus* Knox, 1950. Knox's species has not been validated by the citation of type specimen and locality.

Occurrence.—Hardinsburg formation, locality TCO-153; rare.

Genus PUNCTATI-SPORITES (Ibrahim) Schopf, Wilson & Bentall, 1944

Description.—Spores radial, trilete; original spherical or subspherical shape often reflected by a lack of proximal-distal orientation and heavy arcuate folds resulting from oblique compression; ornamentation various; trilete suture simple or with well developed lips, rays of variable length, in some instances extending to spore margin; spore coat variable in thickness, translucent to transparent. Known size range, 27–120 microns.

Genotype.—*Punctati-sporites punctatus* (Ibrahim) Ibrahim, 1933.

Remarks.—There is little doubt that this genus includes not only spores of different natural affinities but also many form elements which might well be separated from it on the basis of ornamentation. At the present time, its geologic range (as observed at The Carter Oil Research Laboratory) extends from the Devonian to the Recent. This wide stratigraphic range is due largely to the diverse elements which constitute the genus. These elements include many useful guide species as well as others of potential stratigraphic value. Form genera based on ornamentation are used by Ibrahim, R. Potonie, Kremp, and other German workers. Splitting of this genus should be done with extreme caution. Many apiculate and echinate forms presently included within the genus can, however, owing to their quite distinctive ornamentation, be separated from *Punctati-sporites*. The authors therefore follow the usage of Potonie and Kremp (1954) in assigning circular forms with large, blunt, crowded, more or less conical processes to *Apiculati-sporites* (Ibrahim) Potonie and Kremp, 1954, and those bearing crowded thin spines to *Acanthotriletes* (Naumova) Potonie and Kremp, 1954.

PUNCTATI-SPORITES? BACCATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 2

Description.—Spores radial, trilete; outline circular to subcircular; arcuate compression folds occasional; spore margin irregular; ornamentation numerous variable tuberculate processes, length 0.5–1.7 microns, basal diameter 0.8–1.6 microns, tapered to narrow rounded tips; trilete suture two-thirds to full spore radius, usually raised ridges, or a series of tuberculations in line; spore coat thin, translucent to transparent in non-tuberculate areas; diameter, 26–46 microns.

Holotype.—TCO-82, 2075 ft., slide 8, ser. 19,087, Hardinsburg formation; diameter 29 microns.

Remarks.—The small size and beaded surface of the spore are characteristic. Fig. 16 (unnamed spore), p. 158, in Knox (1948) illustrates a similar form.

Occurrence.—Hardinsburg formation; localities TCO-82, TCO-153, TCO-143 No. 1, 2, 3, 5; common. TCO-108, Waltersburg formation; common.

PUNCTATI-SPORITES? CALLOSUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 39, fig. 7

Description.—Spores radial, trilete; circular to subcircular in proximal view; generally proximo-distally oriented, arcuate compression folds occasional; spore coat smooth; trilete rays distinct, simple, approximately two-thirds spore radius; spore coat translucent to transparent, approximately 2 microns thick, color brown; diameter 50–65 microns.

Holotype.—TCO-82, 2078 ft., slide 2, ser. 15,769, Hardinsburg formation; 58×65 microns.

Remarks.—Examination of specimens under phase contrast showed a true wall thickness of approximately 2 microns. This species is similar to *Calamospora* (?) *obesus* (Loose) Schopf, Wilson and Bentall, 1944, but the latter has a diameter of 97–160 microns.

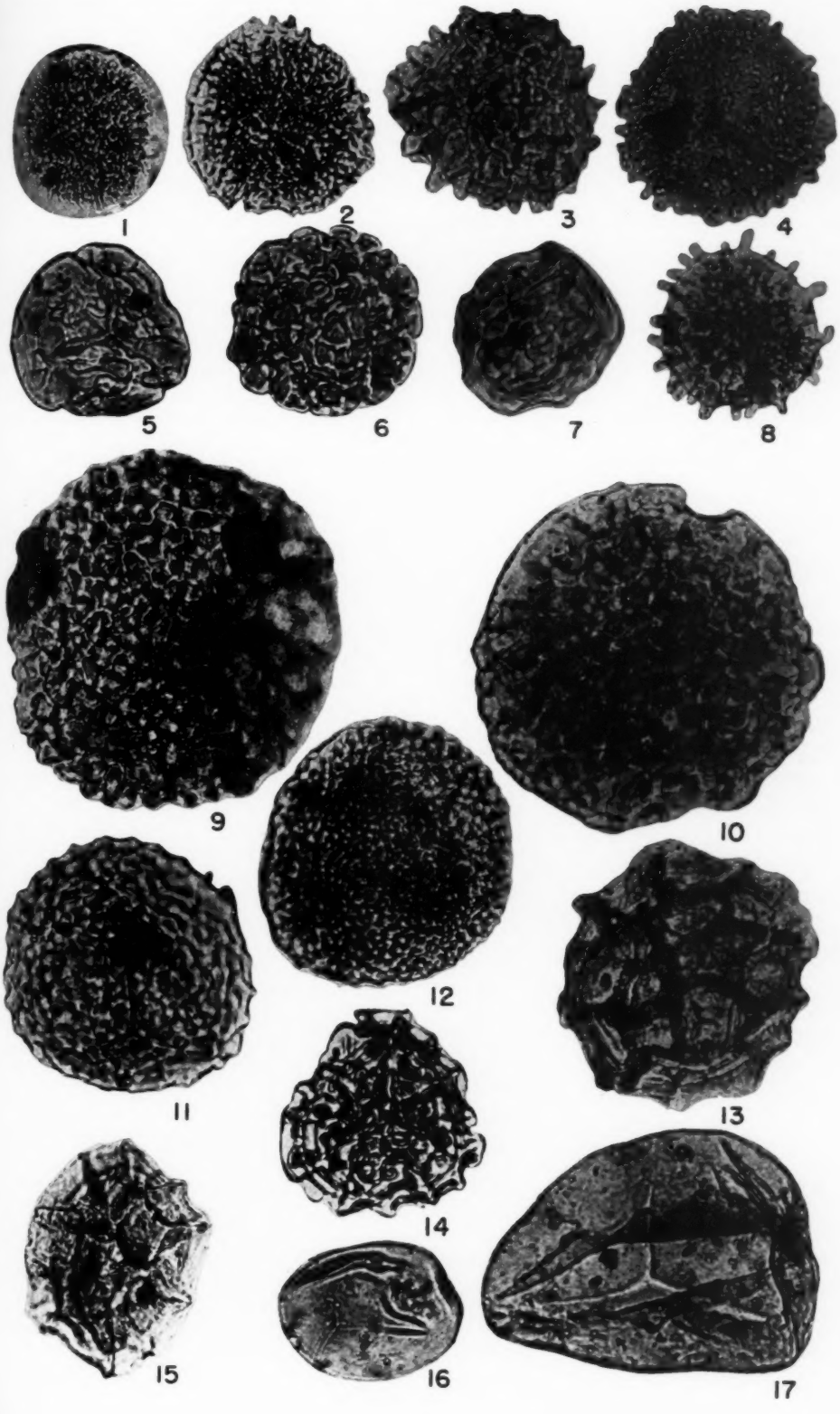
Occurrence. — Hardinsburg formation, TCO-82; occasional.

PUNCTATI-SPORITES? CEROSUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 6

Description.—Spores radial, trilete; form originally spherical; ornamentation poorly defined granulations simulating tubercles at the equator; trilete sutures simple, approximately two-thirds of the spore radius; spore coat translucent, approximately 3 microns thick, waxy luster; compressed

EXPLANATION OF PLATE 38

FIGS. *1*, *2*—*Acanthotriletes echinatus* Hoffmeister, Staplin and Malloy, n. sp.; *1*, holotype, 33.6×35.7 microns; *2*, 44×46 microns, TCO-82, ser. 16,481. (p. 379)
3—*Apiculati-sporites pineatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 48.3×50.4 microns. (p. 381)
4—*Punctati-sporites?* type A; 53 microns. (p. 394)
5, *6*—*Convolutispora florida* Hoffmeister, Staplin and Malloy, n. sp.; *5*, 40×43 microns, flattened specimen showing trilete, TCO-82, ser. 18,683; *6*, holotype, 49 microns. (p. 384)
7—*Convolutispora* type A; 43.5 microns. (p. 385)
8—*Raistrickia multipertica* Hoffmeister, Staplin and Malloy, n. sp., holotype; 40×42 microns excluding spines. (p. 395)
9—*Convolutispora tessellata* Hoffmeister, Staplin and Malloy, n. sp., holotype; 86 microns. (p. 385)
10—*Convolutispora mellita* Hoffmeister, Staplin and Malloy, n. sp., holotype; 82×84 microns. (p. 384)
11—*Convolutispora venusta* Hoffmeister, Staplin and Malloy, n. sp., holotype; 61.6 microns. (p. 385)
12—*Convolutispora ampla* Hoffmeister, Staplin and Malloy, n. sp., holotype; 62×64 microns. (p. 384)
13—*Reticulati-sporites* type A; 65 microns, TCO-82, ser. 15,809. (p. 395)
14—*Reticulati-sporites* type B; 48×53 microns. (p. 395)
15—*Reticulati-sporites decoratus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 48×57 microns. (p. 395)
16—*Calamospora* cf. *C. straminea* Wilson and Kosanke, 1944; 35.7×44 microns, TCO-153, ser. 19,418. (p. 382)
17—*Calamospora* type A; 61×84 microns. (p. 382)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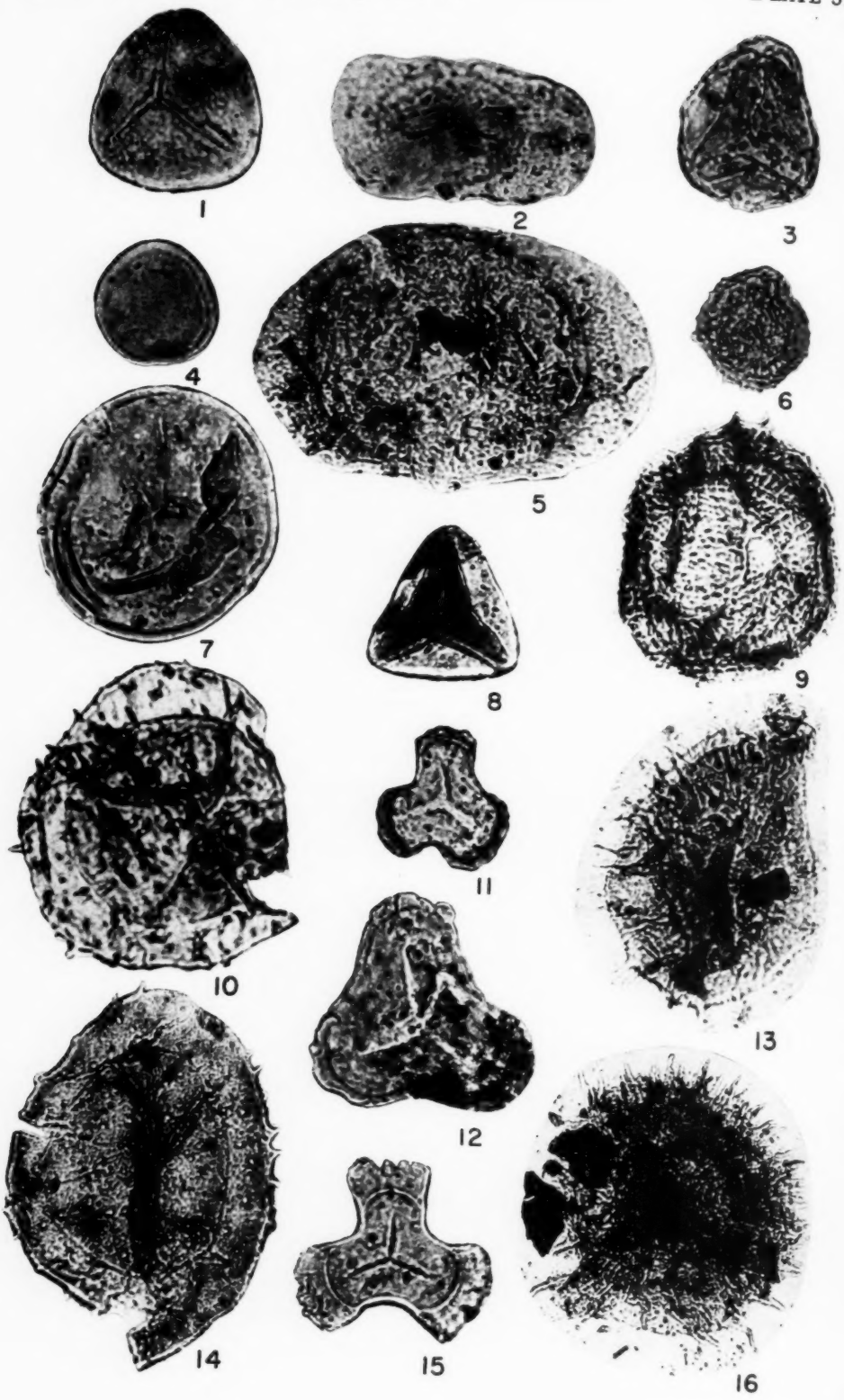
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zone near equator appears smooth; diameter 37–53 microns.

Holotype.—TCO-82, 2071 ft., slide 10, ser. 18,823, Hardinsburg formation; 48 microns.

Remarks.—This species is distinguished from others of the genus by its waxy luster and irregular uneven surface.

Occurrence. — Hardinsburg formation, TCO-82; rare.

PUNCTATI-SPORITES FISSUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 8

Description.—Spores radial, trilete; form originally spherical, arcuate compression folds common; surface distinctly granular; suture length approximately one-half spore radius, trilete area often split open and folded; spore coat thin, translucent to transparent; diameter 50–61 microns.

Holotype.—TCO-82, 2071 ft., slide 3, ser. 18,778, Hardinsburg formation; 57×61 microns.

Remarks.—This species is common in all samples except TCO-143, locality 3. The trilete suture commonly is torn open because of the thin somewhat fragile spore coat.

PUNCTATI-SPORITES GRANDIS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 7

Description.—Spores radial, trilete; form originally spherical, arcuate compression folds common, no preferred orientation; ornamentation scattered variable tuberculate to conical processes 1.0–2.1 microns long, 3–8 microns apart, remainder of surface smooth or faintly punctate; trilete sutures approximately two-thirds spore radius, sometimes involved in the folding; spore coat moderately thick, translucent; diameter 92–120 microns.

Holotype.—TCO-82, 2085 ft., slide 4, ser. 19,020, Hardinsburg formation; 120 microns.

Remarks.—The large size and numerous small processes characterize this species.

Occurrence.—Hardinsburg formation, locality TCO-82; occasional.

PUNCTATI-SPORITES NITIDUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 4

Description.—Spores radial, trilete; outline circular, arcuate compression folds common; surface levigate to faintly granulose; trilete sutures simple, approximately two-thirds spore radius; spore coat translucent, approximately 2 microns thick; diameter 31–43 microns.

Holotype.—TCO-82, 2072, ft., slide 9, ser. 18,659, Hardinsburg formation; 34 microns.

Remarks.—This species is somewhat generalized in character but can be distinguished by its relatively thick wall and small size. It is relatively abundant when encountered.

EXPLANATION OF PLATE 39

FIG. *1*—*Punctati-sporites?* type C; 42 microns. (p. 394)
2—*Schulzospora elongata* Hoffmeister, Staplin and Malloy, n. sp., holotype; 30.5×60.8 microns. (p. 396)
3—*Rotaspora fracta* Schemel, 1950; 36×38 microns. (p. 396)
4—Spore type C; 30 microns. (p. 398)
5—*Schulzospora* cf. *S. rara* Kosanke, 1950; 63.2×98.3 microns, TCO-82, ser. 18,623. (p. 396)
6—*Punctati-sporites?* type B; 29 microns. (p. 394)
7—*Punctati-sporites? callosus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 58×65 microns. (p. 392)
8—Spore type E; 38 microns. (p. 398)
9—Incertae sedis; 95.2×106.4 microns. (p. 398)
10, 14—*Grandispora spinosa* Hoffmeister, Staplin and Malloy, n. sp.; *10*, holotype, 118 microns; *14*, 111×165 microns, TCO-82, ser. 18,807. (p. 388)
11—*Triquitrites* type A; 28.5×31 microns. (p. 397)
12—*Triquitrites marginatus* Hoffmeister, Staplin and Malloy, n. sp., holotype; 45.8×49.3 microns. (p. 397)
13—Spore type D; 57×78 microns, TCO-82, ser. 18,765. (p. 398)
15—*Tripartites vetustus* Schemel, 1950; 43 microns, TCO-82, ser. 18,807. (p. 397)
16—Spore type D; 105 microns, TCO-82, ser. 19,472. (p. 398)

Occurrence. — Hardinsburg formation, TCO-82, TCO-153, and TCO-143, locality 5; common to abundant.

PUNCTATI-SPORITES PLICATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, figs. 9, 10

Description.—Spores radial, trilete; outline roughly circular but all specimens folded; ornamentation finely but distinctly papillate; trilete sutures indistinct or absent; spore coat very thin, translucent to transparent, color light amber yellow; diameter 24–45 microns.

Holotype.—TCO-155 No. 3, slide 4, ser. 19,373, Hardinsburg formation (Pl. 36, fig. 9); 38×43 microns.

Remarks.—Well-preserved specimens of this form are rare, probably because of the thin spore coat. It would be placed in *Punctati-sporites* Ibrahim, 1933, in the classification of Potonie and Kremp.

Occurrence. — Hardinsburg formation, TCO-82, TCO-153, TCO-143 No. 1; common.

PUNCTATI-SPORITES PSEUDOLEVATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 5

Description.—Spores radial, trilete; form originally spherical; arcuate compression folds common; ornamentation finely granulose, more pronounced on larger specimens; sutures distinct, length approximately two-thirds spore radius; spore coat subtransparent, approximately 2 microns thick; diameter 50–74 microns.

Holotype.—TCO-83, 2071 ft., slide 1, ser. 15,920, Hardinsburg formation; 61 microns.

Remarks.—This species is characterized by its thick wall with heavy arcuate folding and finely granulose surface.

Occurrence.—Hardinsburg formation, TCO-82, TCO-153 and TCO-143, localities 1 and 2; occasional.

PUNCTATI-SPORITES RETICULOPUNCTATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 36, fig. 1

Description.—Spores radial, trilete; form originally spherical; outline slightly crenulate because of folding; spore coat strongly punctate, punctations crowded, subcircular, 1.0 to 1.6 microns in diameter; trilete sutures distinct, lips narrow, approximately two-thirds spore radius; spore coat translucent, approximately 2.5 to 3 microns thick; diameter, 35–57 microns.

Holotype.—TCO-143 No. 5, slide 10, ser 19,320, Hardinsburg formation; 53×57 microns.

Remarks.—The distinct trilete, smaller pits, and smaller spore size distinguish this species from *P. fenestratus* Kosanke and Brokaw, (in Kosanke 1950).

Occurrence.—Hardinsburg formation, localities TCO-153, TCO-143 No. 3, 5; occasional.

PUNCTATI-SPORITES? type A
Pl. 38, fig. 4

Description.—Spore radial, trilete; outline circular; ornamentation scattered short cylindrical processes, tips bluntly rounded, diameter 2 microns, length 3–4 microns, remainder of spore coat finely granulose; trilete rays distinct, simple, approximately two-thirds spore radius; spore coat moderately thick, translucent; diameter 53 microns.

Remarks.—One specimen, TCO-82, 2071 ft., slide 8, ser. 18,812, Hardinsburg formation.

PUNCTATI-SPORITES? type B
Pl. 39, fig. 6

Description.—Spore radial, trilete; outline subcircular, margin irregular, appearing in part apiculate; ornamentation subreticulate, ridges vermiculate, interrupted, width 1 micron, depressed areas irregular; trilete not distinct, lips raised, two-thirds spore radius; spore coat thickness moderate, translucent, color amber yellow; diameter 29 microns.

Remarks.—One specimen, TCO-82, 2077 ft., slide 3, ser. 15,683, Hardinsburg formation.

PUNCTATI-SPORITES? type C
Pl. 39, fig. 1

Description.—Spore radial, trilete; outline convexly subtriangular; ornamentation minutely granulose-punctate; trilete distinct, lips raised, three-fourths spore radius; spore coat translucent, color amber yellow; diameter 42 microns.

Remarks.—One specimen, TCO-82, 2085 ft., slide 1, ser. 15,960, Hardinsburg forma-

tion. This form is questionably assigned to the genus *Punctati-sporites*.

Genus RAISTRICKIA Schopf, Wilson & Bentall, 1944

Description.—Spores radial, trilete; proximal outline circular to subcircular or subdeltoid; original shape probably subspherical; ornamentation heavy well-separated cylindrical or irregular processes, usually blunt and often partate at tips; trilete rays variable in length, usually simple; spore coat thickness moderate, translucent to transparent; diameter 37–90 microns.

Genotype.—*R. grovensis* Schopf (in Schopf, Wilson and Bentall, 1944).

Remarks.—The genus *Raistrickia* is poorly represented in the Hardinsburg samples discussed here, both in numbers and species. This is the first record of its presence in Mississippian rocks of North America.

RAISTRICKIA MULTIPERTICA Hoffmeister, Staplin & Malloy, n. sp.
Pl. 38, fig. 8

Description.—Spores radial, trilete; outline subcircular, folding of spore coat rare; ornamentation blunt cylindrical processes, diameter variable, slightly broader near tips, traces of partation on some spines; spines approximately 4.5 microns apart near equator, more crowded toward the poles. surface of both spore coat and spines levigate; trilete rays distinct, simple, slightly more than two-thirds spore radius; diameter 40–44 microns excluding spines, spines 2.5–5.9 microns.

Holotype.—TCO-153 No. 3, 2325 ft., slide 3, ser. 19,356, Hardinsburg formation; size excluding spines 40×42 microns, spines 1.5–2.5 microns in diameter, 2.5–4.4 microns long.

Remarks.—This species differs from *R. aculeolata* Wilson and Kosanke, 1944, from the Des Moines series of Iowa, in having thinner, more regularly arranged spines and also in its smaller over-all diameter.

Occurrence.—Hardinsburg formation, TCO-153; rare.

Genus RETICULATI-SPORITES (Ibrahim) Schopf, Wilson & Bentall, 1944

Description.—Spores radial, trilete; spherical to oblate; proximal view circular to subcircular, margin irregular because of high muri (reticulate ridges); folding not common; ornamentation coarsely reticulate, variable; in some forms the body wall may also be punctate; trilete rays variable, lips and commissure generally indistinct; spore coat variable in thickness because of muri; size range 40–126 microns.

Genotype.—*R. reticulatus* Ibrahim, 1933.

Remarks.—Forms with a low reticulate network (reticulum) on the spore coat are excluded from the genus. *Microreticulati-sporites fundatus*, n. sp., lacks the highly developed muri.

RETICULATI-SPORITES DECORATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 38, fig. 15

Description.—Spores radial, trilete; outline subcircular; ornamentation strong muri arranged in a reticulum; muri very high simulating a thin membrane which appears to be involved in the development of the muri; trilete obscure; spore coat translucent, thickness variable; diameter 48–60 microns, muri 4–6 microns high, diameter of lacunae 8–12 microns.

Holotype.—TCO-82, 2075 ft., slide 7, ser. 19,084, Hardinsburg formation; 48×57 microns.

Occurrence.—Hardinsburg formation, locality TCO-82; rare.

RETICULATI-SPORITES type A
Pl. 38, fig. 13

Description.—Spore radial, trilete; outline circular; ornamentation heavy muri arranged in a reticulum, height 5 microns, width 3–5 microns, lacunae variable in size and shape, diameter 8–13 microns; trilete simple, distinct, three-fourths spore radius; spore coat translucent, amber brown, thickness variable; diameter 56–65 microns.

Remarks.—Hardinsburg formation, TCO-82, 2072 ft., slide 5, ser. 15,809 (Pl. 38, fig. 13); 2087–2088 ft.. slide 2, ser. 18,831.

RETICULATI-SPORITES type B
Pl. 38, fig. 14

Description.—Spore radial, trilete; outline subcircular; proximal ornamentation heavy vermiculate to anastomosing ridges, width approximately 3 microns, height 4 microns,

ridges partly knobbed, a few knobs 3–3.5 microns in diameter not connected to ridges; distal ornamentation more regularly reticulate; ridges high, simulating a membrane appearing intimately connected with ridges; trilete distinct, four-fifths spore radius; spore coat translucent, amber brown, thickness extremely variable; size 48×53 microns.

Remarks.—One specimen, TCO-82, 2080–80.5 ft., slide 4, ser. 16,439, Hardinsburg formation.

Genus ROTASPORA Schemel, 1950

Description.—Spores radial, trilete; proximal view circular to subtriangular; central body triangular; radial margins convex, inter-radial margins convex or concave; equatorial flange broadest at inter-radial positions, thickened at periphery to a narrow rim; surface levigate, punctate, granulose; trilete rays slightly shorter than radius, lips not modified; size range 28–46 microns.

ROTASPORA FRACTA Schemel, 1950
Pl. 39, fig. 3

Rotaspora fracta SCHEMEL, 1950, Jour. Paleontology, vol. 24, p. 242, pl. 40, figs. 8–9.

Remarks.—One specimen of *Rotaspora*, apparently conspecific with this species, was found in TCO-82, 2079.4 ft., slide 2, ser. 15,847, Hardinsburg formation; 36×38 micons.

Genus SCHULZOSPORA Kosanke, 1950

Description.—Spores radial, trilete; appear bilateral because of elliptical bladder, commonly compressed in good proximal-distal orientation; central body spherical, bladder apparently completely encloses the central body; ornamentation of body and bladder identical, punctate to slightly granulose; trilete often obscure, lips not developed; spore coat and bladder thin, translucent to transparent; size range 60–120 microns.

Genotype.—Schulzospora rara Kosanke, 1950.

Remarks.—The following species has been described from Tournaisian-Viséan rocks of the U.S.S.R.:

Schulzospora campyloptera (Waltz) Hoffmeister, Staplin and Malloy, n. comb. *Zonotriletes campylopterus* Waltz, 1938; in Luber and Waltz, 1938, Trans. Cent. Geol. and Prospecting Inst., Fasc. 105, p. 16, pl. 3, fig. 39, pl. A, fig. 15.

SCHULZOSPORA ELONGATA Hoffmeister, Staplin & Malloy, n. sp.
Pl. 39, fig. 2

Description.—Spores radial, trilete; outline elongate-oval; central body enclosed by bladder; bladder faintly folded; ornamentation central body smooth to slightly granulose, bladder granulose to finely reticulate; trilete rays distinct, approximately three-fourths central body radius; central body coat moderately thick, translucent, bladder coat very thin, transparent; size 30–61 microns.

Holotype.—TCO-82, 2072 ft., slide 1, ser. 15,800, Hardinsburg formation; size 60.8×30.5 microns, central body 35×25.7 microns.

Remarks.—The extremely elongate shape characterizes this species.

Occurrence.—Hardinsburg formation, localities TCO-82, TCO-143 No. 1; occasional.

SCHULZOSPORA cf. S. RARA Kosanke, 1950
Pl. 39, fig. 5

Schulzospora rara KOSANKE, 1950, Illinois State Geol. Survey, Bull. 74, pp. 53–54, pl. 13, figs. 5–8.

Remarks.—Hardinsburg specimens are smaller than those found by Kosanke in the Battery Rock coal of Illinois. Figured specimen, 98.3×63.2 microns, central body 60.8×70.2 microns; TCO-82, 2072 ft., ser. 18,623, Hardinsburg formation.

Occurrence.—Hardinsburg formation, TCO-82, TCO-153, TCO-143 No. 2, 5; common.

Genus TRIPARTITES Schemel, 1950

Description.—Spores radial, trilete; proximal view subtriangular, interradial margins usually concave; sublenticular in axial view; equatorial flange widest at the radial margins, narrow or absent at the interradial margins, fluted or plicate in the widest portions; ornamentation smooth to verrucose, not always uniform over central body and flange; trilete rays confined to central body, usually distinct, lips absent or moderate; spore coat translucent, flange sometimes thicker than central body wall; size range 30–70 microns.

Remarks.—The genotype of *Triquitrites* (*T. arculatus* Wilson and Coe, 1940) possesses a flange around the entire margin. Broad fluting of the flange at the radial positions is

therefore the major characteristic of *Tripartites.*

TRIPARTITES VETUSTUS Schemel, 1950
Pl. 39, fig. 15

Tripartites vetustus SCHEMEL, 1950, Jour. Paleontology, vol. 24, p. 243, pl. 40, fig. 11.

Remarks.—The size range of the Hardinsburg specimens is 30–37 microns, almost duplicating the size range of 30–40 microns for specimens described by Schemel. TCO-82, 2071 ft., slide 7, ser. 18,807 (Pl. 39, fig. 15), Hardinsburg formation. Also TCO-143, No. 5; occasional in both localities.

Genus TRIQUITRITES Wilson & Coe, 1940

Description.—Spores radial, trilete; triangular in outline, corners rounded or truncate subangular, interradial areas slightly convex to strongly concave, spore coat of radial areas thickened; a narrow flange, partial or entire, may be present; ornamentation levigate, granulose, verrucose; trilete rays variable, generally extended nearly to thickened areas, lips faint to thick and prominent, arcuate ridges lacking; spore coat thickness variable; size range 30–70 microns.

Genotype.—Triquitrites arculatus Wilson and Coe, 1940.

Remarks.—The genotype of *Triquitrites* possesses a definite flange, slightly wider at the radial positions, around the entire spore body. *Tripartites* Schemel differs only in that the flange is very broad and fluted at the radial positions. *Triquitrites* range from the Upper Mississippian to the Upper Pennsylvanian, while *Tripartites* is known only from Mississippian rocks.

TRIQUITRITES MARGINATUS Hoffmeister, Staplin & Malloy, n. sp.
Pl. 39, fig. 12

Description.—Spores radial, trilete; axial view sublenticular; proximal view subtriangular, radial margins convex, interradial margins concave; equatorial flange distinct, widest at radial margins, narrow or absent at the interradial margins; central body levigate, flange faintly fluted, thicker than central body; trilete rays distinct, simple, almost equal to central body radius; spore coat relatively thick, lacking conspicuous folding, translucent; size range 42–61 microns, flange at radial positions 5.6–11 microns.

Holotype.—TCO-82, 2072 ft., slide 1, ser. 15,789, Hardinsburg formation; size 45.8× 49.3 microns, flange 2.0–5.6 microns.

Remarks.—Triquitrites marginatus has less blunt radial areas and more pronounced flange development than *T. arculatus* Wilson and Coe, 1940.

Occurrence.—Hardinsburg formation, localities TCO-82, TCO-143 No. 5; occasional.

TRIQUITRITES type A
Pl. 39. fig. 11

Description.—Spore radial, trilete; proximal view subtriangular, corners convex, inter-radial margins concave; equatorial flange widest at radial margins, with an undulating surface and irregular margin at its widest points; size 28.5×31 microns, flange width 1–4 microns; ornamentation, spore body probably levigate, the slight irregularities due to maceration, flange levigate; trilete simple, without lips; length 11.3–12.5 microns; central body thin and transparent, flange relatively thick and translucent.

Remarks.—One specimen, TCO-82, 2071 ft., slide 1, ser. 15,923, Hardinsburg formation. The thinner central body and the smaller size distinguish this form from *Triquitrites marginatus,* n. sp.

Genus indeterminate
Spore type A
Pl. 37, fig. 9

Description.—Spore radial, trilete; outline subtriangular, folding absent; ornamentation scattered small tubercules on a smooth to faintly granulose surface; trilete suture prominent, lips strongly raised into ridges extending as thickenings to the equatorial margin; distal surface apparently thickened except for the outer 10.5 microns of the spore radius; spore coat translucent; diameter, 67 microns.

Remarks.—Because of its subtriangular shape and the strong lip development of the long trilete rays, this form resembles the illustration of *Endosporites* type A of Schemel (1950) from the Upper Mississippian (?) of Utah. One specimen, TCO-82, 2072 ft., slide 5, ser. 15,823, Hardinsburg formation.

Spore type B
Pl. 37, fig. 10

Description.—Spore radial, trilete; subcircular in outline; size 80×86 microns; cen-

tral spore body 46 microns in diameter, enclosed by a heavy equatorial girdle approximately 12 microns wide; distally three bands of thickening 12–19 microns wide radiate from spore axis to join the girdle, but fork to form three additional thin areas near the girdle; central body granular, remainder of spore coat smooth; trilete rays distinct, simple, length approximately one-half spore radius; spore coat subtransparent.

Remarks.—This species resembles the "Spore type B" of Schemel (1950) from Daggett County, Utah. One specimen, TCO-82, 2076 ft., slide 6, ser. 19,884, Hardinsburg formation.

Spore type C
Pl. 39, fig. 4

Description.—Spores radial, alete (?); outline circular; probable spherical shape indicated by arcuate compression fold near margin; surface smooth or finely punctate; trilete markings not evident; spore coat relatively thick, translucent; diameter 30 microns.

Remarks.—Two specimens: TCO-82, 2078 ft., slide 1, ser. 15,756 (Pl. 39, fig. 4); 2071 ft., slide 1, ser. 15,919, Hardinsburg formation.

Spore type D
Pl. 39, figs. 13, 16

Description.—Spores radial, assumed trilete; outline subcircular; diameter 78–105 microns excluding processes; ornamentation crowded very large spines 10–20 microns in length, radiating from the spore body; trilete not noted; spore coat translucent, thicker in central area.

Remarks.—Two specimens; TCO-82, 2071 ft., slide 10, ser. 19,472 (Pl. 39, fig. 16); 2078 ft., slide 10, ser. 18,765 (Pl. 39, fig. 13). Hardinsburg formation. Unusually long spines characterize this form.

Spore type E
Pl. 39, fig. 8

Description.—Spore radial, trilete; outline deltoid, radial apices slightly rounded; surface of spore faintly granular, trilete suture strongly developed, rays extending nearly the full spore radius, lips prominently developed, 8.4 microns wide at junction of rays, tapering to 2 microns at ends. Over-all diameter 38 microns.

Remarks.—One specimen, Hardinsburg formation, TCO-82, 2087–88 ft., slide 1, ser. 16,531.

Incertae Sedis
Pl. 39, fig. 9

Description.—Unknown plant (?) structure; no germinal suture; outline subcircular, wall folded concentrically and provided with thin subparallel ridges, 2.8–5.6 microns apart, occasionally bifurcating or joining and arranged in an irregular radiating manner best developed near the periphery; ridges project from the margin giving the effect of spines; wall thin, amber colored, translucent to transparent; diameter, 106.4×95.2 microns.

Remarks.—One specimen, TCO-82, 2078 ft., slide 2, ser. 15,180, Hardinsburg formation. In outline and color this form resembles a plant spore, but no suggestion of a germinal suture could be found and the surface ornamentation is unlike that of any known spore.

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MIDDLE CRETACEOUS GASTROPODA FROM PUNTA CHINA, BAJA CALIFORNIA, MEXICO[1]

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ABSTRACT—Richly fossiliferous Middle Cretaceous sediments occur on the Pacific coast of Baja California, Mexico. Sediments of this age are represented by a 160 meter thick section of the Alisitos formation exposed at Punta China, approximately 120 kilometers south of the United States boundary. There two lithologically distinct members can be recognized: an upper member composed principally of biohermal limestones with interbedded coarsely pyroclastic sediments, and a lower member composed almost entirely of fine sediments. The Punta China section is unconformably overlain by late Upper Cretaceous and Quaternary deposits.

The fauna of the Alisitos formation at Punta China is characterized by caprinid pelecypods, corals, and cerithiid and nerineid gastropods. Fifty-four species and varieties of the Gastropoda, 28 of them new, are described in detail and figured. Tentatively identified and listed are 73 species representing the more prominent pelecypods, brachiopods, bryozoans, corals, echinoderms, ostracodes, and Foraminifera.

In contrast to provincial Middle Cretaceous faunas further north, the Punta China fauna includes cosmopolitan elements. The gastropods *Tectus* (*Tectus*) *texanus* (Roemer), *Turritella* (*Haustator*) aff. *T.* (*H.*) *seriatim-granulata* Roemer, *Semineritina apparata* (Cragin), *Pyrazus* (*Echinobathra*) *austinense* (Roemer), *Tylostoma* (*Tylostoma*) *mutabilis* Gabb, *Liocarenus* (*Liocarenus*) *formosum* (Cragin), and *Actaeonella parvus* (Stanton) occur in Texas and adjacent parts of Central America and the Caribbean, indicating marine communication with the Pacific during Middle Cretaceous times. *Otostoma* (*Lyosoma*) *japonica* (Nagao), *Cimolithium miyakoense* (Nagao), *Natica importuna* Nagao, and *Natica japonica* (Nagao) are Japanese species. *Microschiza* (*Cloughtonia*) *scalaris* (Conrad) and *Actaeonella fusiformis* Coquand occur in the Mediterranean region. Recognition of the Foraminifera *Orbitolina texana* (Roemer) in the Alisitos formation provides the first record of this widely distributed species on the West Coast of North America.

Faunal studies thus far completed suggest a middle Albian age for at least the upper member of the Punta China section of the Alisitos formation. The environmentally and faunally distinct lower member may represent a similar age or may be as old as Aptian.

New species and varieties described are: *Agnathodonta brooksi*, *Anchura* (*Anchura*) *andersoni*, *A.* (*Perissoptera*) *hannai*, *Angaria* (*Angaria*) *gwynae*, *Cassiope* (*Cassiope*) *kleinpelli*, *C.* (*Gymnentome*) *gwynae*, *Cerithiopsis stantoni*, *Cerithium? emersoni*, *Cimolithium eleanorae*, *C. miyakoense* (Nagao) var. *tomásensis*, *Cirsochilus gilberti*, *Encycloscala emersoni*, *Euthriofusus wenzi*, *Keilostoma quaidei*, *Mesalia* (*Mesalia*) *mauryae*, *Nerinea* (*Plesioptygmatis*) *bösei*, *N.* (*P.*) *tomásensis*, *Neritoma* (*Neridomus*) *woodfordi*, *N.* (*N.*) *delpeyae*, *Oligoptycha? popenoei*, *Pseudonerinea stantoni*, *P. stirtoni*, *Pyrazus* (*Echinobathra*) *durhami*, *Pyrazus? harrissi*, *Tectus* (*Tectus*) *tomásensis*, *Tectus? thalmanni*, *Turritella? durhami*, *Uchauxia beali*, *U. kirki*.

INTRODUCTION

HIGHLY fossiliferous Middle Cretaceous sediments occur in the vicinity of Puerto Santo Tomás, about 120 kilometers south of the international boundary along the Pacific Coast of Baja California. The fauna, particularly as represented in the sea cliff outcrops of Punta China, is well preserved, is greatly diversified, and in contrast to more northern Pacific Coast faunas, contains many cosmopolitan elements. Hence it is of unusual interest.

The presence of Middle Cretaceous strata along the western side of the peninsula of Baja California has been recognized since at least 1913 (Böse and Wittich, 1913) but a paucity of readily available and accurately refined geologic and paleontologic data has tended to obscure the significance of this oc-

[1] Contribution from the Museum of Paleontology, University of California, Berkeley.

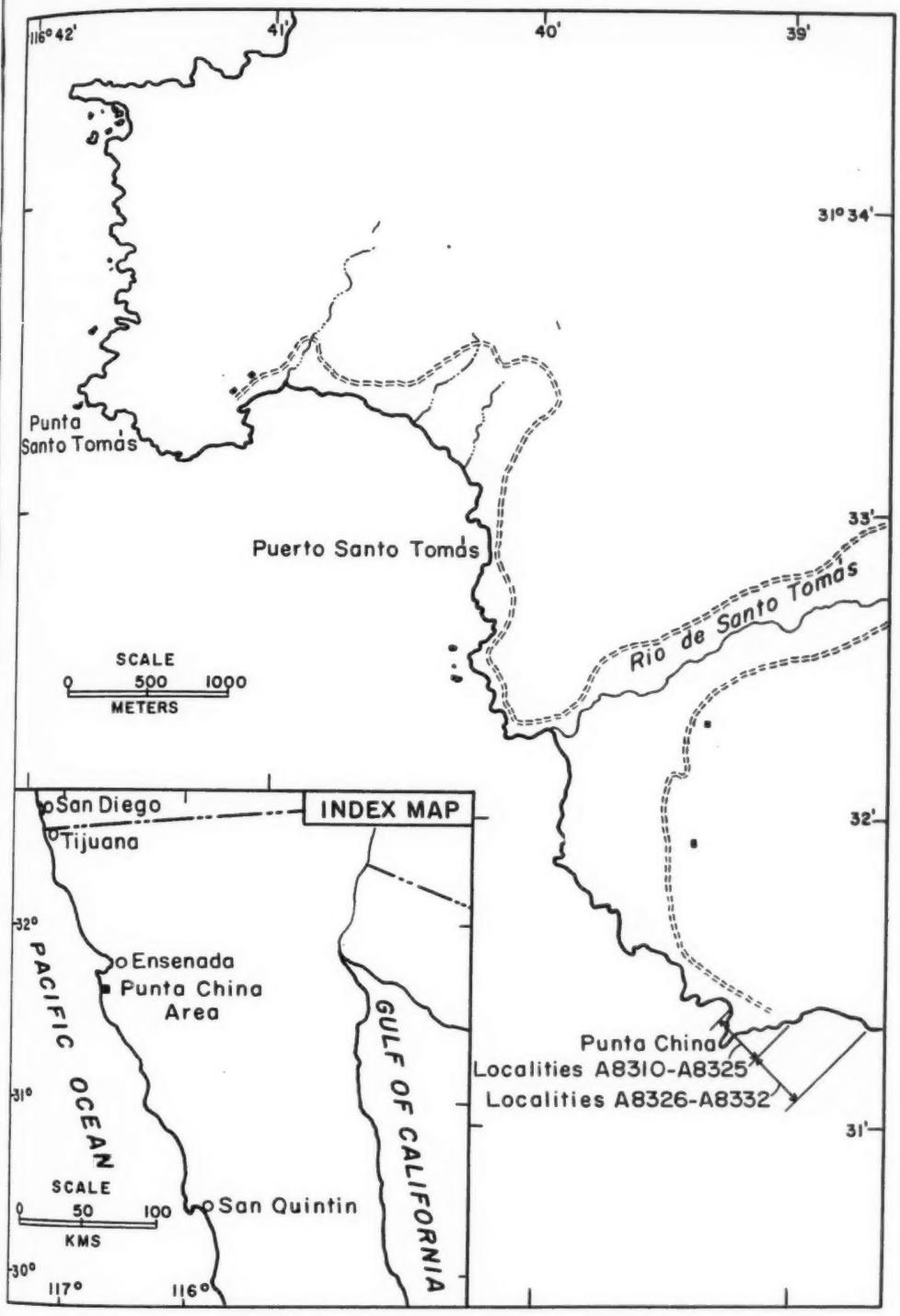


FIG. 1—Generalized map of Punta China and vicinity, Baja California, Mexico.

currence. A reconnaissance study by two University of California students (Kirk and MacIntyre, 1951) was instrumental in directing the author's attention to this area. Their report dealt principally with Middle Cretaceous outcrops at Punta San Isidro, approximately 40 kilometers to the south of Punta China.

The gastropods, with which the present work is concerned, and associated invertebrates were collected along the shore line of Punta China where a sequence of Middle Cretaceous strata is consistently well exposed. All of the fossils collected during several short field trips have been deposited in the Museum of Paleontology, University of California at Berkeley.

This report was prepared in partial fulfillment of requirements for the degree of Master of Arts, Department of Paleontology, University of California. Many people have offered advice and encouragement during its preparation; the author is especially grateful for the generous and patient assistance given by Dr. J. Wyatt Durham.

GEOLOGY

The Middle Cretaceous rocks at Punta China and in adjacent areas are characterized by a predominantly volcanic (andesitic) aspect, the chief rock types being volcanic breccias and porphyritic flows with interbedded tuffaceous sediments and biohermal limestones. The geographic distribution of the volcanics has not yet been traced with certainty but similar associations of volcanic and pyroclastic rocks exhibit similar stratigraphic and tectonic relationships in the Santa Ana Mountains of Southern California and south along the western side of the peninsular range at least to the Santa Clara Desert of Baja California, Mexico.

Several formational names have been used in Baja California for units which appear to be at least partially equivalent to the Punta China Middle Cretaceous sequence. The "Fernando formation" (Anon., 1924; Beal, 1948) and the "San Telmo formation" (Woodford and Harriss, 1938) are two such names. A third, the "Alisitos formation," is directly applicable to the strata of Punta China. Although when originally proposed by Santillán and Barrera (1930, pp. 9, 10) the Alisitos formation was identified as older than Middle Cretaceous, Punta China is clearly within the small type area mapped by those authors.

The Lower Cretaceous age assigned the Alisitos formation by Santillán and Barrera was based on very few fossils. Disagreement with conclusions reached in the present work may be in part due to incorrect identifications. Another possible explanation of the discrepancy may be that strata included in the type locality for the Alisitos formation represent a greater time span than can now be recognized.

The Alisitos formation in its type area attains a thickness of at least several thousand meters but only approximately 160 meters of continuously exposed section (Text-fig. 2) at Punta China were systematically examined for this study. Two members are about equally represented in the measured section. The upper member (including fossil localities A-8310 to A-8325) is composed principally of andesitic flows, breccias, and interbedded bioherms. This member is underlain by a slightly lesser thickness (including fossil localities A-8326 to A-8332) of reddish to greenish dark tuffaceous sediments. Though not absolute, this twofold division of general lithologic types is clearly expressed in the physiography of the area: by deep erosion in in the poorly consolidated graywackes and silts of the lower member and by positive geomorphic features representing the volcanic-limestone member above.

The nature of the rocks immediately underlying the Alisitos formation is not yet known but phyllites, argillites, quartzites, and other metasediments observed in the western foothills of the peninsular range may occupy this position. The emplacement of the diorites and quartz diorites which make up the bulk of the peninsular range plutonic core probably occurred at the same time as the vulcanism responsible for the Middle Cretaceous volcanic sequence (Hirschi and Quervain, 1927, 1928). East of Punta China the plutonics reportedly intrude these volvanics and their associated bioherms (Böse and Wittich, 1913; Woodford and Harriss, 1938).

A narrow, eastward-thinning wedge of almost flat-lying, poorly consolidated Upper

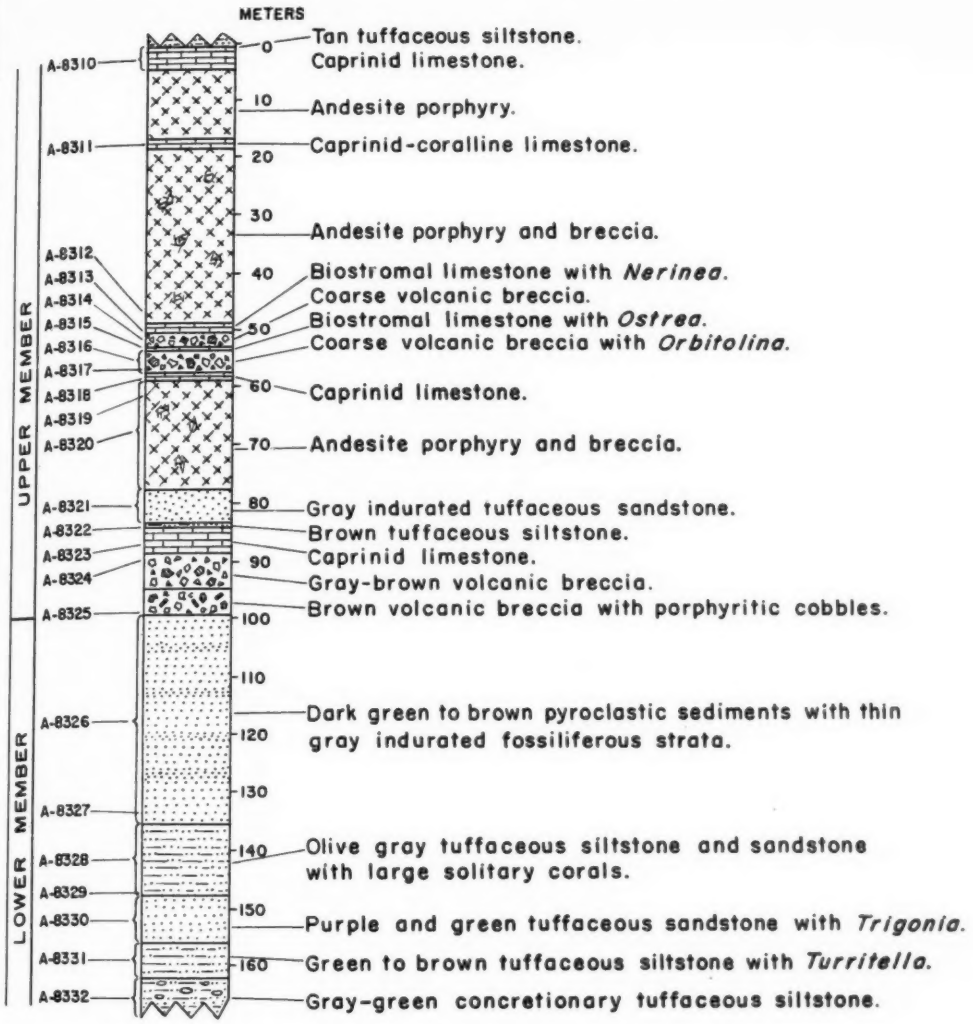


FIG. 2—Columnar section of Alisitos formation at Punta China.

Cretaceous silts, sandstones, and conglomerates, the Rosario formation (Anon., 1924; Beal, 1948) of probable Maestrichtian age (Durham and Kirk, 1950), overlies the steeply westward dipping Middle Cretaceous section at Punta China. The more coarsely clastic phases of the Rosario formation are deposited on and against a topographic high of resistant Alisitos rocks at Punta China indicating that the point existed in late Cretaceous times as a physiographic feature. Specimens of *Coralliochama orcutti* White occur commonly in these sediments. Southward from Punta China the Rosario formation is characterized by dark gray silty shales and siltstones with cephalopods (including *Baculites inornatus* Meek, *Nostoceras sternbergi* Anderson and Hanna, and *Eutrephoceras* sp.) and a microfauna dominated by *Vaginulina* cf. *V. daini* Schijfsma, *Nodosaria velascoense* Cushman, *Dentalina marcki* Reuss (?), *Dentalina solvata* Cushman, *Loxostoma*

plaitum (Carsey), and *Valvulineria cretacea* (Carsey).

A Quaternary terrace deposit is the only other lithogenetic unit recognized at Punta China. Fossiliferous sediments preserved on the south side of the point at an elevation of about 25 feet contain a fauna including elements, such as *Cryptochiton stelleri* (Middendorff) and *Balanophyllia elegans* Verrill, which are usually found living at present north of Point Conception, California.

BIOSTRATIGRAPHY AND CORRELATION

The two members of the Alisitos formation at Punta China are distinguished by two faunas, faunas so different in both general and specific aspects that they could easily be mistakenly interpreted as unrelated. Burrowing pelecypods, solitary corals, brachiopods, echinoids, crinoids, Foraminifera, ostracodes, and such gastropods as *Turritella* and *Actaeonella* dominate the sandy and silty horizons of the lower member. Sessile pelecypods, colonial corals, and cerithiid and nerineid gastropods are abundant in the typical biohermal assemblage of the upper member. Appearances and disappearances of individual species in the local section at Punta China appear to have resulted from major environmental changes rather than from the rise or extinction of those species within the period of time represented by the section.

Despite the great diversity and abundance of the faunas from the Alisitos formation at Punta China, no ammonites have yet been found. Correlation of these beds with the European Cretaceous sequence is therefore greatly hindered. Wide dispersal and relatively well understood phylogenies have made ammonites the basis of most Mesozoic intercontinental correlations. A Middle Cretaceous climatic and geographic setting favorable for wide dispersal of organisms other than ammonites is manifested in the Punta China occurrence of several exotic species, notably the gastropods identified as *Microschiza* (*Cloughtonia*) *scalaris* (Conrad) and *Actaeonella fusiformis* Coquand which also occur in Europe and North Africa. Unlike many ammonites, however, these species have poorly known geologic ranges.

In order to establish the age of the Punta China faunas, comparisons were made with faunas elsewhere whose relationships to the European standard were already established. Relatively well known Middle Cretaceous faunas of Texas and related Gulf Coast areas have many species in common with the Alisitos formation. A significant guide fossil occurring in both areas, *Orbitolina texana* (Roemer), indicates that the Punta China beds are no older than Aptian and no younger than middle Albian. *Seminerita apparata* (Cragin), *Pyrazus* (*Echinobathra*) *austinense* (Roemer), and *Liocarenus* (*Liocarenus*) *formosum* (Cragin) of the Punta China section appear to be confined to strata of middle Albian age in Texas and adjacent regions. Occurrences of these species through the upper portion of the studied section are interpreted as indicative of a middle Albian age for that part of the section.

Faunas from the lower part, although fully as rich, are less definitive. They perhaps correspond approximately in age to the very different faunas of the upper member or are possibly as old as Aptain.

The bioherms of the Alisitos formation are composed principally of caprinids, usually *Caprinuloidea perfecta* Palmer. A very similar geologic situation appears on the island of Cuba where caprinid reefs of the Provincial limestone are associated with andesitic pyroclastics and flows of the Tuff formation (MacGillavry, 1937). MacGillavry considered the Provincial limestone, as well as the closely related caprinid faunas of southern Mexico (Palmer, 1928) to be middle Albian in age. A Cenomanian age assignment used by Palmer was based on a comparison of the American caprinids to related genera from strata in the Italian Alps and on the island of Sicily which at that time were considered Cenomanian in age. However, the occurrence of species at Punta China which are known to be of middle Albian age elsewhere demonstrates that at least some of the American caprinid limestones were deposited during middle Albian time.

The faunas of Punta San Isidro (Kirk and MacIntyre, 1951), located about 40 kilometers south of Punta China, represent an environment and age approximately equivalent to the section under consideration. *Orbitolina texana* (Roemer) and *Aptyxiella* (*Endiatrachelus*) *parallela* (Anderson and Hanna) are among the fossils common to both Punta

San Isidro and Punta China.

In a reference which usually has been overlooked by geologists working in Baja California, Böse and Cavins (1927, pp. 86–87) pointed out the wide extent of the Middle Albian caprinid reef facies through the Central American province. They indicated that the Baja California sequence of andesitic volcanics and caprinid limestones and the similar sequence at Arivechi, Sonora, (Imlay, 1944b, pp. 1186–1187) represent shallow water deposits of the same middle Albian sea. Geographic isolation of this extensive Central American province from its near-by contemporary western North American province as suggested by F. M. Anderson (1938, p. 84) now appears improbable. The absence of known species common to the two provinces is probably due to severe environmental differences, the dissimilarity being exaggerated by the lack of information on chronologically equivalent faunas of western North America.

The impressive similarity of the widely separated Middle Cretaceous faunas in Asia, in the Mediterranean region, and in the Americas indicates relatively unobstructed marine communication, though the means of organic dispersal are difficult to outline. The present distribution of Middle Cretaceous marine sediments suggests that shallow seas extended over large areas within present continental margins. Submarine research in the central Pacific (Hamilton, 1953) has recently demonstrated the existence of islands or shallow banks during Middle Cretaceous times which supported rich populations of reef corals, echinoids, molluscs, and stromatoporoids. Successive radiations of the planktonic stages of stenobathic organisms from a series of such shallow water centers may have provided a means by which individual species could cross broad oceanic basins.

ECOLOGY

A spectacular feature of the middle Albian deposits at Punta China is the fine preservation exhibited by many of the fossils. Despite the coarseness of some of the volcanic breccias, fragile tests of Foraminifera, echinoids, and small molluscs are almost perfectly preserved. Pelecypods almost always occur with both valves intact. Some gastropod species [*Cimolithium miyakoense* (Nagao), *Nerinea* (*Plesioptygmatis*) *bösei* n. sp., *Natica importuna* Nagao, and *Natica japonica* (Nagao)] retain original pigmentation. Even a slight amount of reworking of such sediments would destroy the less robust elements of this association and disassociate pelecypod valves. For this reason the depositional environment appears to have been one in which periodic volcanic explosions showered pyroclastic debris over nearby marine areas, burying in situ the living organisms.

The composition of the Punta China faunas suggests a shallow water tropical environment. Reef corals (*Montastrea*, *Isastrea*, *Astrocoenia*, *Myriophyllia*, etc.) of the upper member certainly represent water depths of less than 50 meters and temperatures no cooler than 18.5°C. (Vaughan and Wells, 1943). Very abundant turritellas in the finer clastic deposits of the lower member probably indicate that the water was no deeper than 100 meters (Merriam, 1941, pp. 14–16). Differences in the faunal content of the two members can be attributed principally to differences in the substrata on which the organisms existed. The sediments forming the substrate varied with the volcanic materials being deposited. Middle Cretaceous faunas known from California which are almost completely dissimilar to the Baja California faunas occur in normal clastic sedimentary sequences suggesting that the nature of the substratum as well as the mode of deposition of the sediments serve as important controls over the faunal composition.

DESCRIPTION OF FOSSIL LOCALITIES

All locality numbers refer to the collections of the Museum of Paleontology of the University of California at Berkeley, California.

The following data pertain to all localities (A-8310 through A-8332):

Stratigraphic position: Alisitos formation (Aptian—middle Albian).

Location: Shore of Punta China, approximately two kilometers south of mouth of Río de Santo Tomás, northwestern Baja California, Mexico.

Map Reference: A.A.F. Preliminary Base, Ensenada (472 B), scale 1:500,000, April, 1946.

Approximate attitude of strata: Dip 20° to 30° W., strike N. 10° E.

A-8310: Uppermost caprinid limestone exposed at Punta China (north side). Fauna consists principally of caprinids, corals, oysters, and a few nerineas.

A-8311: Second caprinid limestone exposed at Punta China, approximately 12 meters stratigraphically below uppermost caprinid limestone (loc. A-8310).

A-8312: Dark volcanic breccia approximately 30 meters stratigraphically below second caprinid limestone (loc. A-8311), and immediately above biostrome composed of *Nerinea* (loc. A-8313). Fauna consists mostly of *Nerinea* (*Plesioptygmatis*) *tomásensis* n. sp.

A-8313: Biostrome composed almost entirely of *Nerinea* (*Plesioptygmatis*) *tomásensis* n. sp. cropping out in small cove on north side of main Punta China promontory. Approximately 7 meters stratigraphically above caprinid limestone (loc. A-8318) which is third such limestone downward from top of section.

A-8314: Dark volcanic breccia containing

Check List of Middle Cretaceous Gastropoda from Punta China

	Localities																							
	A-8310	A-8311	A-8312	A-8313	A-8314	A-8315	A-8316	A-8317	A-8318	A-8319	A-8320	A-8321	A-8322	A-8323	A-8324	A-8325	A-8326	A-8327	A-8328	A-8329	A-8330	A-8331	A-8332
Calliostoma (*Calliostoma*) aff. *C.* (*C.*) *cragini* Stanton																						F	
Tectus (*Tectus*) *texanus* (Roemer)												R											
Tectus (*Tectus*) *tomásensis* n. sp.								R															
Tectus (?) *thalmanni* n. sp.												R											
Agnathodonta brooksi n. sp.								R															
Encycloscala emersoni n. sp.																						C	
Cirsochilus gilberti n. sp.							R																
Angaria (*Angaria*) *gwynae* n. sp.												R											
Microschiza (*Cloughtonia*) *scalaris* (Conrad)																						F	
Neritoma (*Neridomus*) *woodfordi* n. sp.							R																
Neritoma (*Neridomus*) *delpeyae* n. sp.								R															
Otostoma (*Lyosoma*) *japonica* (Nagao)								C															
Semineritina apparata (Cragin)								F															
Keilostoma quaidei n. sp.												R											
Mesalia (*Mesalia*) *mauryae* n. sp.																						C	
Turritella (*Haustator*) aff. *T.* (*H.*) *seriatimgranulata* (Roemer)																						A	A
Turritella (?) *durhami* n. sp.																						F	
Cassiope (*Cassiope*) *kleinpelli* n. sp.																						A	
Cassiope (*Gymnentome*) *gwynae* n. sp.																						A	
Omalaxis planorbis (Roemer) (?)								R															
Metacerithium sp.																						F	
Uchauxia kirki n. sp.								C				C											
Uchauxia beali n. sp.								C				C											
Cimolithium miyakoense (Nagao)								C				C											
Cimolithium miyakoense (Nagao) var. *tomásensis* n. var.								F															
Cimolithium eleanorae n. sp.								C				F											
Pyrazus (*Echinobathra*) *austinense* (Roemer)								F															
Pyrazus (*Echinobathra*) *durhami* n. sp.								R				C										F	
Pyrazus (?) *harrissi* n. sp.								R															
Cerithium (?) *emersoni* n. sp.												R											
Cerithiopsis (?) *stantoni* n. sp.												C											
Cerithiella (*Cerithiella*) *kickapooense* (Stanton) (?)																						C	
Amaea (*Confusiscala*) sp.																						R	
Opalia (*Crassiscala*) *riachuelanum* (Maury)																						F	
Pseudonerinea stantoni n. sp.																						C	
Pseudonerinea stirtoni n. sp.																						A	A
Nerinea (*Plesioptygmatis*) cf. *N.* (*P.*) *pseudoconvexa* Stanton								F				C											
Nerinea (*Plesioptygmatis*) *bösei* n. sp.				C				F				C											
Nerinea (*Plesioptygmatis*) *tomásensis* n. sp.			F	A	C	F	R	F						C									
Aptyxiella (*Aptyxiella*) cf. *A.* (*A.*) *subula* (Roemer)								F				F											
Aptyxiella (*Endiatrachelus*) *parallela* (Anderson and Hanna)												F	F									C	
Cossmannea (*Eunerinea*) *pauli* (Coquand)	R																						
Diozoptyxis cf. *D. pilgrimi* (Cox)		R																					
Anchura (*Anchura*) *andersoni* n. sp.																						C	
Anchura (*Perissoptera*) *hannai* n. sp.								?				F											
Natica importuna Nagao								F				A											
Natica japonica (Nagao)																						A	
Tylostoma (*Tylostoma*) *mutabilis* Gabb								C															
Tylostoma (*Tylostoma*) cf. *T.* (*T.*) *materinum* White												F											
Euthriofusus wenzi n. sp.																						C	
Liocarenus (*Liocarenus*) *formosum* (Cragin)								R															
Actaeonella parvus (Stanton)								F															
Actaeonella fusiformis Coquand					?																	A	
Oligoptycha (?) *popenoei* n. sp.																						R	

a few large molluscs, underlying *Nerinea* biostrome (loc. A-8313).

A-8315: Biostrome composed of *Ostrea* with abundant nerineas at top. Approximately 3 meters stratigraphically above caprinid limestone (loc. A-8318) which is third such limestone downward from top of Punta China Middle Cretaceous section.

A-8316: Dark volcanic breccia containing reworked molluscs and corals. Immediately underlies *Ostrea* biostrome (loc. A-8315).

A-8317: Poorly sorted dark volcanic breccia overlying the third caprinid limestone (loc. A-8318) downward from top of Punta China section. Abundant and diverse fauna characterized by *Orbitolina texana*, *Pygopyrina* sp., reef corals, and many molluscan species.

A-8318: Third caprinid limestone downward from top of section. Approximately 3 meters thick and 50 meters stratigraphically below highest caprinid limestone (loc. A-8310).

A-8319: Blue tuffaceous sandstone containing large pelecypods, and bundles of serpulid worm tubes. Approximately 2 meters stratigraphically below third caprinid limestone (loc. A-8318).

A-8320: Interbedded andesite porphyry and proclastics, the latter containing very few poorly preserved molluscs, 3 to 17 meters stratigraphically below third caprinid limestone (loc. A-8318).

A-8321: Compact gray tuffaceous sandstone with large coral and molluscan fauna similar to that at locality A-8317. Approximately 4 meters stratigraphically above lowest caprinid limestone (loc. A-8323), the fourth such limestone downward from top of Punta China section. On south side of point.

A-8322: Brown weathered tuffaceous siltstone approximately 1 meter wide and immediately overlying lowest caprinid limestone (loc. A-8323) on south side of Punta China. Fauna dominated by very small molluscs and solitary corals.

A-8323: Lowest caprinid limestone of Punta China section. Contains caprinids, reef corals and large inflated echinoid spines.

A-8324: Dark volcanic breccia immediately underlying lowest caprinid limestone (loc. A-8323), with large oysters and nerineas.

A-8325: Dark pyroclastics consisting of rounded andesitic cobbles in matrix of volcanic breccia, 6 to 8 meters stratigraphically below lowest caprinid limestone (loc. A-8323) exposed on Punta China. Fauna dominated by attached pelecypods, corals, and echinoids.

A-8326: Several thin beds of dark gray tuffaceous sandstone interbedded with coarse pebbly pyroclastics. Exposed about half way between tip of Punta China and base of point on south side, 10 to 50 meters stratigraphically below lowest caprinid limestone (loc. A-8323). Fauna consists mainly of pelecypods (*Lima*, *Plicatula*, and *Neithea*), rhynchonellid brachiopods, and worm tubes.

A-8327: Dark gray compact tuffaceous grit containing large, heavy-shelled pelecypods. Stratigraphically approximately 40 meters below lowest caprinid limestone (loc. A-8323) on south side of Punta China.

A-8328: Gray-green shale, siltstone, and sandstone containing large solitary corals. Approximately 6 meters stratigraphically above prominent purple tuffaceous sandstone (loc. A-8330).

A-8329: Dark tuffaceous sandstone containing large pelecypods, 1 or 2 meters stratigraphically above purple tuffaceous sandstone (loc. A-8330).

A-8330: Purple, pooly consolidated tuffaceous sandstone containing *Trigonia* aff. *T. weaveri* Stoyanow. Approximately 10 to 20 meters stratigraphically above lowest Middle Cretaceous strata exposed along southern shoreline of Punta China.

A-8331: Moderately well consolidated, massive, gray-green to brown tuffaceous siltstone with abundant and well preserved molluscs. *Turritella* (*Haustator*) aff. *T.* (*H.*) *seriatim-granulata* Roemer is especially abundant. Approximately 10 to 15 meters stratigraphically above lowest Middle Cretaceous exposures along south side of Punta China.

A-8332: Gray-green to brown interbedded tuffaceous siltstone and silty shale exposed to about 10 meters stratigraphically above base of Middle Cretaceous section exposed along south side of Punta China. Foraminifera and ostracode fauna associated with *Turritella*, *Pseudonerinea*, and solitary corals.

	Localities																					
	A-8310	A-8311	A-8312	A-8313	A-8314	A-8315	A-8316	A-8317	A-8318	A-8319	A-8320	A-8321	A-8322	A-8323	A-8324	A-8325	A-8326	A-8327	A-8328	A-8329	A-8330	A-8331	A-8332
Foraminifera:																							
Hyperammina (?) sp.																							R
Ammodiscus incertus (d'Orbigny)																							C
Textularia chapmani Lalicker (?) *Nubecularia depressa* Chapman																							R
Globulina exserta (Berthelin)																							F
Guttulina exepolita Bullard																							R
Lenticulina cf. *L. subalta* (Reuss)								?															A
Lenticulina sp.																							F
Saracenaria bononiensis var. *striatolipa* Tappan																							F
Saracenaria sp.																							R
Astacolus nuda (Reuss)																							F
Vaginulinopsis sp.																							R
Vaginulina debilis (Berthelin)																							C
Vaginulina kochii Roemer																							R
Darbyella (?) sp.																							F
Dentalina sp.																							R
Nodosaria orthopleura Reuss																							R
Nodosaria sceptrum Reuss																							C
Nodosaria sp.																							A
Höglundina carpenteri (Reuss)																							R
Epistomina (?) *cretosa* Dam																							A
Orbitolina texana (Roemer)[1]								C															R
Tristix acutangulum (Reuss)																							R
Discorbis (?) sp.																							C
Valvulineria sp.																							R
Ceratobulimina woodi Khan																							R
Cibicides (?) sp.																							R
Porifera:																							
Cliona sp.								C															
Coelenterata:																							
Astrocoenia sp.								R				F											
Cyathophora sp.												A											
Myriophyllia cf. *M. cuyleri* (Wells)								C															
Dermosmilia sp.												C											
Isastrea whitneyi Wells		A						C											A	C	A	A	
Montlivaltia sp.																							
Montastrea sp.		C						F				F							F			A	
Placosmilia sp.																							
Annelida:																							
Serpula aff. *S. socialis* Goldfuss													A										
Echinodermata:																							
Crinoid columnals (pentagonal)																							
Holectypus (*Coenholectypus*) *planatus* Roemer																R							
Pygopyrina sp.								C															
Enallaster texanus (Roemer) (?)												R											
Bryozoa:																							
Reptomulticava sp.																			R			R	
Brachiopoda:																							
Rhynchonellid brachiopods																	C						
Ostracoda:																							
Cytheropteron trinitiensis (Vanderpool) (?)																						F	
Loxoconcha (?) sp.																						R	
Bairdia sp.																						R	
Haplocytheridea (?) sp.																						C	
Cytherella sp.																						A	
Paracypris sp.																						C	
Pelecypoda:																							
Caprinuloidea sp.	A	A					C	A			C		A										
Ostrea (*Lopha*) *subovata* Schumard						F																	
Ostrea (*Arctostrea*) *carinata* Lamarck				F								C											
Gryphaea mucronata Gabb															A								
Gryphaea wardi Hill and Vaughan							C								R								
Exogyra yabei Nagao				F			F								C								
Exogyra cf. *E. quitmanensis* Cragin							R								F								
Lima (*Mantellum*) sp.																R							
Lima wacoensis Roemer							R									A	A						
Neithea aff. *N. occidentalis* Conrad																							
Neithea aff. *N. wrighti* (Shumard)							R																
Plicatula sp.							R																
Linearia sp.									R														
Ptychomya densicostata Nagao (?)									R														
Cucullaea sp.										R													
Trigonia stolleyi Hill										R							R					R	
Trigonia aff. *T. weaveri* Stoyanow																				C			
Corbula sp.							R																
Protocardia stonei Cragin																						R	
Protocardia (?) sp.																	R						
Intergricardium (?) sp.																						F	
Resatrix sp.																						C	
Scaphopoda:																							
Dentalium sp.																						C	
Decapoda:																							
Crab fragments												C											

[1] Nine specimens, Hypotype nos. 40, 245–40, 254, are in the Univ. Calif. Museum Paleontology.

Punta China Gastropoda—Reported Occurrences in Other Areas

	Aptian	Albian			Cenomanian
		Lower	Middle	Upper	
Tectus (*Tectus*) *texanus* (Roemer)			— NA —		
Microschiza (*Cloughtonia*) *scalaris* (Conrad)			— Af —		
Otostoma (*Lyosoma*) *japonica* (Nagao)			— As —		
Semineritina apparata (Cragin)			— NA —		
Turritella (*Haustator*) aff. *T.* (*H.*) *seriatimgranulata* Roemer			— NA —		
Cimolithium miyakoense (Nagao)			— As —		
Pyrazus (*Echinobathra*) *austinense* (Roemer)			— NA —		
Opalia (*Crassiscala*) *riachuelanum* (Maury)			— SA —		
Aptyxiella (*Endiatrachelus*) *parallela* (Anderson and Hanna)	— ? As	&	NA —		
Cossmannea (*Eunerinea*) *pauli* (Coquand)		— Af	&	NA —	
Natica importuna Nagao			— As —		
Natica japonia (Nagao)			— As —		
Liocarenus (*Liocarenus*) *formosum* (Cragin)			— NA	&	? Af —
Actaeonella parvus (Stanton)			— NA —		
Actaeonella fusiformis Coquand	– E & Af –				

Af Africa
As Asia
NA North America
SA South America
E Europe

SYSTEMATICS

This study has been pursued with the intention of providing the soundest possible basis for further investigations of the Baja California Middle Cretaceous geology. The fossils here considered are therefore only those which were collected from the single, approximately 160 meter thick, section at Punta China where adequate exposures provide reasonable assurance that the succession of strata is free from faults or other unrecognized complicating factors.

The large size of the Punta China collections and the limited time available for study have imposed further limitations on the scope of this work. Though the collections are extremely diverse, only one group, the Gastropoda, is treated systematically; the other expressed identifications are preliminary only. A number of gastropod species either too poorly preserved for reasonable identification or too large to be readily collected in the field are likewise omitted.

Gastropod species were identified in most cases by reference to type figures or subsequent figures of type specimens and topotypes. Unfortunately, except for *Aptyxiella* (*Endiatrachelus*) *parallela* (Anderson and Hanna), specimens were not available for direct comparison.

The classification of the gastropods used in the text is essentially that proposed by Wenz (1938–1940). The availability of more recent data and the reevaluation of typologies necessitates some modification of his system for several groups, such as *Nerinea* and its relatives. Type numbers are those of the Museum of Paleontology, University of California at Berkeley, California, where all of the Punta China material is now housed.

Correlation charts of the Geological Society of America (Stephenson et al., 1942; Imlay, 1944a) have provided nearly all of the age assignments utilized for fossil occurrences in Central America and southern North America. Abundance of individual species in their various stratigraphic occurrences at Punta China is expressed by the symbols (A), (C), (F), and (R), which indicate respectively: Abundant (21 specimens or more collected), Common (6 to 20 specimens), Few (3 to 5 specimens), and Rare (1 or 2 specimens).

Phylum MOLLUSCA
Glass GASTROPODA
Subclass PROSOBRANCHIA
Order ARCHAEOGASTROPODA
Superfamily TROCHACEA
Family TROCHIDAE
Subfamily CALLIOSTOMATINAE
Genus CALLIOSTOMA Swainson

Calliostoma SWAINSON, 1840, Treat. Malac., pp. 218, 351.

Type species (Herrmannsen, 1846 fide Wenz, 1938): *Trochus conulus* Linnaeus.

Subgenus CALLIOSTOMA s. s.
CALLIOSTOMA (CALLIOSTOMA) aff. C. (C.) CRAGINI Stanton
Pl. 40, fig. 4

Hypotype.—No. 33412, loc. A-8331.

Occurrence.—Punta China, loc. A-8331 (F).

Remarks.—Several specimens of this gastropod are known from the lower portion of the measured section at Punta China. They consistently exhibit four tuberculated spiral ridges on the sides of each of the adult whorls. The Punta China form differs from *Calliostoma* (*Calliostoma*) *cragini* Stanton s. s. in this respect; the latter having five such spiral ridges per whorl.

Stanton's species occurs in the Kiowa shale of Comanche (type locality) and Clark Counties, Kansas, and in the Kiamichi formation of Lynn County, Texas. All its known occurrences are middle Albian in age.

Subfamily TROCHINAE
Genus TECTUS Montfort

Tectus MONTFORT, 1810, Conch. Syst.

Type species: *Trochus mauritianus* Gmelin.

Subgenus TECTUS s. s.
TECTUS (TECTUS) TEXANUS (Roemer)
Pl. 40, fig. 1, 2

Trochus texanus ROEMER, 1888, Palaeont. Abh., Band 4, p. 13 (293), pl. 1 (31), fig. 13; ——, ADKINS, 1928, Texas Univ. Bull. 2838, p. 174.
Trochus (*Tectus*) *texanus* Roemer. STANTON, 1947, U. S. Geol. Survey Prof. Paper 211, pp. 57–58, pl. 48, figs. 2–6.

Hypotype.—No. 33413, loc. A-8321.

Occurrence.—Punta China, loc. A-8321 (R).

Remarks.—This species is known elsewhere only from the Edwards limestone (middle Albian) of Travis County, Texas.

TECTUS (TECTUS) TOMÁSENSIS
Allison, n. sp.
Pl. 40, fig. 5

Shell of moderate size, turbinate; spire straight-sided; volutions probably nine; early whorls probably smooth; later whorls concave in profile, each with 15–20 nodes on anterior carina bordering suture; base of body whorl flat, imperforate, smooth; aperture obscured by recrystalization but apparently compressed longitudinally.

Holotype.—No. 33414, loc. A-8317.

Dimensions.—Holotype: height (incomplete) 16.3 mm., diameter (base of body whorl) 14.2 mm., apical angle 52°.

Occurrence.—Punta China, loc. A-8317 (R).

Remarks.—The single imperfectly preserved specimen now available appears to agree in most details with the type species of the genus, *Trochus mauritianus* Gmelin. Its distinctive nodose ornamentation has not been encountered in other recorded Mesozoic species.

TECTUS? THALMANNI Allison, n. sp.
Pl. 40, fig. 3

Shell small, turbinate, rounded anteriorly, imperforate; spire moderately high; volutions seven, evenly convex; ornamentation apparently lacking except for about 12 low ribs separated by narrow interspaces on base of body whorl; aperture large, a low fold on inner lip.

Holotype.—No. 33415, loc. A-8321.

Dimensions.—Holotype: height (incomplete) 6.3 mm., diameter 4.3 mm., apical angle 65°.

Occurrence.—Punta China, loc. A-8321 (R).

Remarks.—This species differs from the much larger *Tectus* (*Tectus*) *texanus*, with which it occurs, by its higher whorl profile, basal spiral ornamentation, and lack of sculpture on spire. The only specimen collected at Punta China is incomplete anteriorly and therefore cannot at present be assigned to the genus *Tectus* with certainty.

Subfamily CHILODONTINAE
Genus AGNATHODONTA Cossmann

Agnathodonta COSSMANN, 1918, Essais Paléonch., tome 11, pp. 200–201.

Type species: *Trochus dentigera* (d'Orbigny).

AGNATHODONTA BROOKSI Allison, n. sp.
Pl. 40, fig. 6

Shell small, massive, moderately high-spired; anteriorly rounded, umbilicate; volutions five or six, evenly convex in profile, whorl diameter about twice corresponding height; sutures distinct; spiral ornamentation of ribs approximately twice as wide as adjacent furrows, increasingly coarse towards umbilicus on base of body whorl; outer lip thick, holostomate; inner lip with single fold inside.

Holotype.—No. 33416, loc. A-8317.

Dimensions.—Holotype: height (complete) 10.0 mm., diameter 7.3 mm., apical angle approximately 45°.

Occurrence.—Punta China, loc. A-8317 (R).

Remarks.—The generic assignment of this species is doubtful but no alternative has been found. A close relationship to Cossmann's genus is suggested by the general shape and spiral ornamentation but the type species of the genus, *Trochus dentigera*, has two folds instead of one fold on the inner lip. In addition, *A. brooksi* exhibits a widely open umbilicus not apparent on the type species.

Family TURBINIDAE
Subfamily LIOTIINAE
Genus ENCYCLOSCALA Cossmann

Encycloscala COSSMANN, 1895, Gastéropodes, Annuaire Géol. Univ. tome 10 (1893), p. 742.

Type species: *Scalaria cretacea* de Boury

ENCYCLOSCALA EMERSONI Allison n. sp.
Pl. 40, figs. 13, 19

Shell small, moderately low-spired; volutions six or seven, whorl diameter about three times height; whorl profile strongly convex; later whorls with 13 strong axial ribs extending to but not crossing sutures; spiral ornamentation of six fine ribs alternating with weaker secondary ribs; base of body whorl with additional spiral ribs and subdued extensions of axial ribs; basal disc indistinct; umbilicus open, bordered by slightly nodose cord with nodes corresponding to axial ribs; aperture ovate, entire, sometimes exhibiting slight tendency to become detached from preceeding whorl.

Holotype.—No. 33417, loc. A-8331. Paratypes: nos. 33419 (fig. 19), 33420–33424, loc. A-8331.

Dimensions.—Holotype: height (incomplete) 8.3 mm., diameter 5.7 mm., apical angle about 45°. Holotype is about average size.

Occurrence.—Punta China, loc. A-8331 (C).

Genus CIRSOCHILUS Cossmann

Cirsochilus COSSMANN, 1888, Ann. Soc. Roy. Malacol. Belgique, tome 3, p. 76.

Type species: *Delphinula striatum* Lamarck

CIRSOCHILUS GILBERTI Allison, n. sp.
Pl. 40, fig. 20

Shell very small, turbinate, low; whorl profile semi-tabulate; volutions four or five, each about one and a half times as large as preceding; spiral ornamentation of three dominant primary ribs, the posterior one most feebly developed, two secondary ribs between the three primaries, and about six additional faint tertiary ribs on posterior surface of whorls; outer lip of aperture thin, slightly flared; base of body whorl with four spiral ribs, slightly weaker than the three primary ribs of whorl; umbilicus closed.

Holotype.—No. 33425, loc. A-8317.

Dimensions.—Holotype: height 4.1 mm., diameter 4.2 mm., apical angle 70° to 80°.

Occurrence.—Punta China, loc. A-8317 (R).

Remarks.—This species is characterized by its low tabulate profile and by the strong arrangement and relative development of its spiral ribs. "*Trochus*" *maestrei* Verneuil and Lorière (1868, pl. 2, fig. 9) from the Aptian of Utrillas, northeastern Spain, lacks the tabulate profile of the Punta China species. The spiral ornamentation of *C. gilberti* is similar to that of the larger and more elevated "*Turbo*" *chihuahuaensis* Böse

(1910, p. 139, pl. 30, figs. 2–4) from the Urgonian of Mexico.

Remarks.—The low whorl profile, slightly developed basal disc, open umbilicus, and strong axial ribs of *E. emersoni* distinguish it from related species. The type species of the genus *Encycloscala*, *Scalaria cretacea*, from the Turonian of France lacks the strong spiral ornamentation of the Baja California species.

Family ANGARIIDAE
Genus ANGARIA Röding

Angaria (Bolten) RÖDING, 1798, Museum Bolten, pt. 2, p. 71.

Type species: *Turbo delphinus* Linnaeus.

Subgenus ANGARIA s. s.

ANGARIA (ANGARIA) GWYNAE Allison, n. sp.
Pl. 40, figs. 7, 8

Shell moderately small, turbinate, depressed; volutions about five, sharply keeled; keel of body whorl with twelve anteriorly directed, toothlike spines; penultimate whorl with approximately 15 such spines; a secondary noded keel anteriorly on last part of body whorl; posterior surface of body whorl broad, slightly concave, apparently with four spiral rows of nodes; prominent innermost row of nodes visible on earlier whorls but outer rows represented only by increasingly finer granular spiral ribs; one additional granular rib present between main and secondary keels on body whorl, six such granular ribs on base between secondary keel and umbilicus; aperture large, angular in outline.

Holotype.—No. 33426, loc. A-8321.

Dimensions.—Holotype: height (almost complete) 9.0 mm., diameter 13.3 mm., apical angle about 90°.

Occurrence.—Punta China, loc. A-8321 (R).

Remarks.—The Baja California species resembles "*Delphinula*" *muricata* and "*Delphinula*" *acuta* of Zekeli (1852, pl. 10, figs. 7a–b and pl. 10, fig. 10, respectively) from the Turonian of Goasu. In both cases, however, the secondary keel (anterior to main keel) is less well developed than on *Angaria* (*Angaria*) *gwynae* thus giving the European species a less angular apertural outline. The European species differ also in the arrangement of their nodose spiral ornamentation.

Superfamily SUBULITACEA
Family PSEUDOMELANIIDAE
Genus MICROSCHIZA Gemmellaro

Microschiza GEMMELLARO, 1878, Giorn. Sci. Nat. Econ. Palermo, vol. 13, p. 135.

Type species (Cossmann, 1909, fide Wenz, 1938): *Turbo philenor* d'Orbigny.

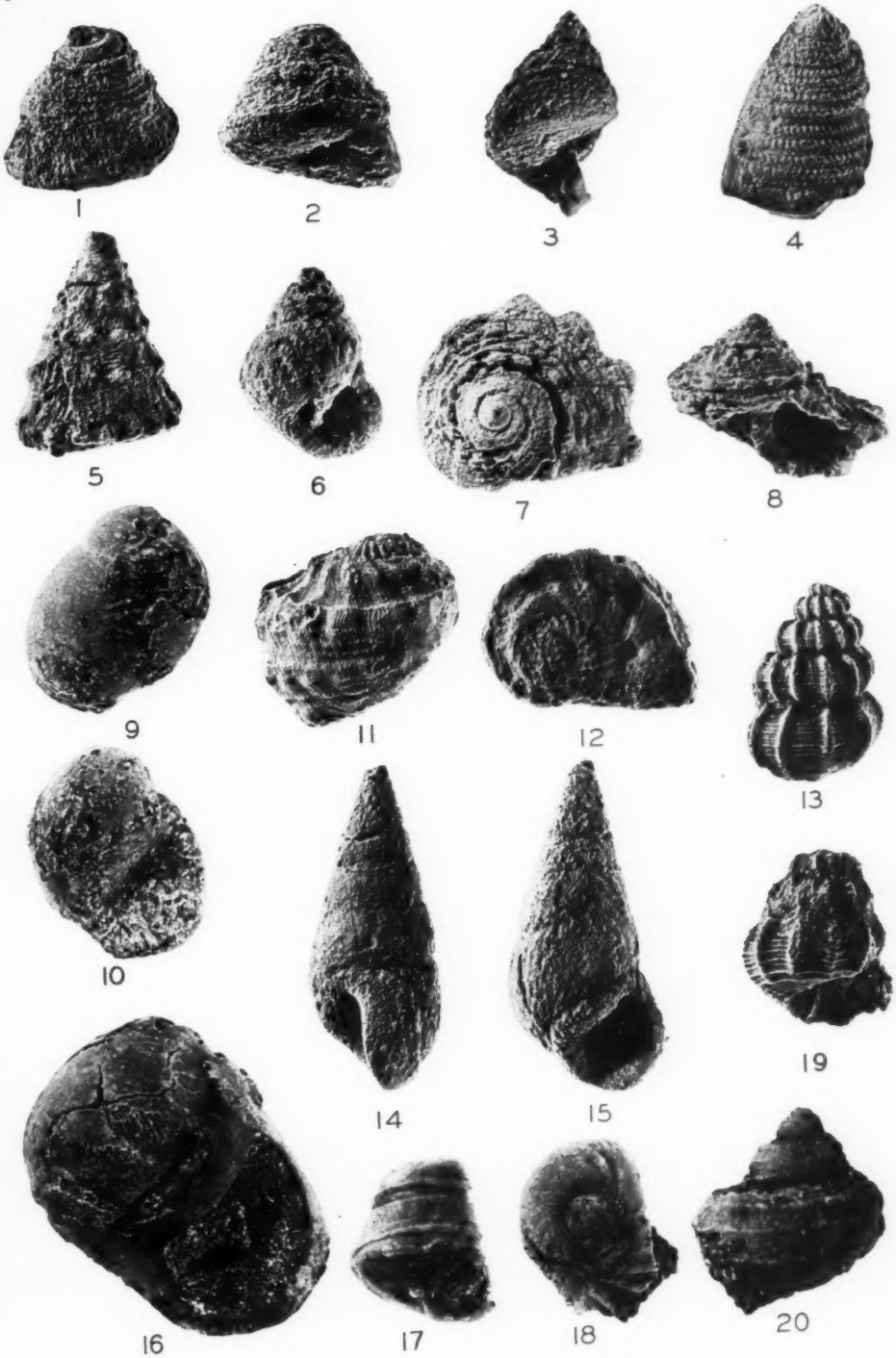
Subgenus CLOUGHTONIA Huddleston

Cloughtonia HUDDLESTON, 1882, Geol. Mag., ser. 2, vol. 9.

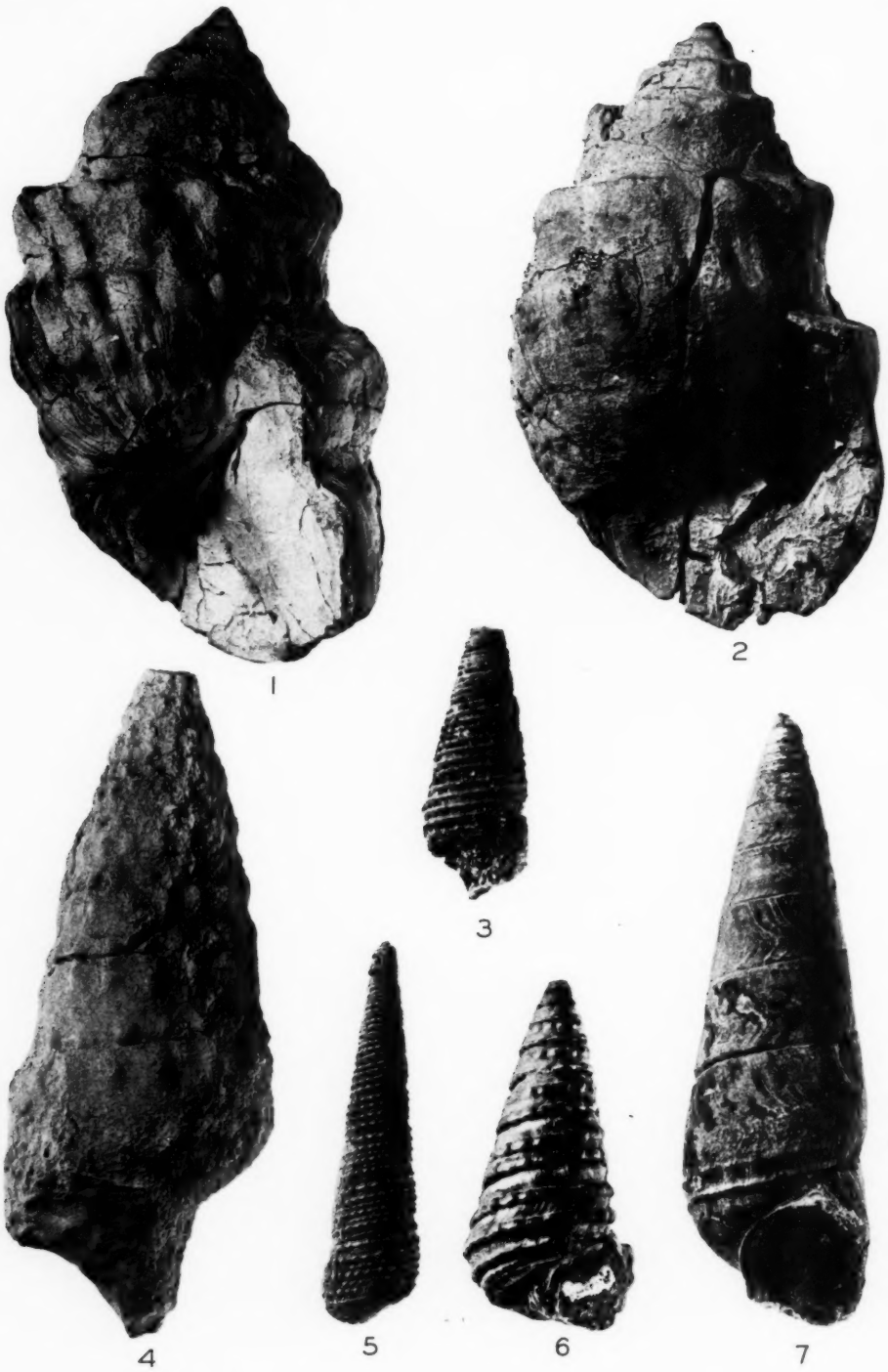
Type species (by monotypy): *Phasianella cincta* Phillips.

EXPLANATION OF PLATE 40

FIGS. *1, 2*—*Tectus* (*Tectus*) *texanus* (Roemer). Hypotype no. 33413, ×1.7. Loc. A-8321. (p. 410)
3—*Tectus? thalmanni* Allison, n. sp. Holotype no. 33415, ×4.4. Loc. A-8321. (p. 410)
4—*Calliostoma* (*Calliostoma*) aff. *C.* (*C.*) *cragini* Stanton. Hypotype no. 33412, ×2.8. Loc. A-8331. (p. 410)
5—*Tectus* (*Tectus*) *tomásensis* Allison, n. sp. Holotype no. 33414, ×1.8. Loc. A-8317. (p. 410)
6—*Agnathodonta brooksi* Allison, n. sp. Holotype no. 33416, ×3.2. Loc. A-8317. (p. 411)
7, 8—*Angaria* (*Angaria*) *gwynae* Allison, n. sp. Holotype no. 33426, ×3.0. Loc. A-8321. (p. 412)
9, 10—*Neritoma* (*Neridomus*) *delpeyae* Allison, n. sp. Holotype no. 33430, ×6.0. Loc. A-8317. (p. 413)
11, 12—*Otostoma* (*Lyosoma*) *japonica* (Nagao). Hypotype no. 33409, ×1.6. Loc. A-8317. (p. 414)
13—*Encycloscala emersoni* Allison, n. sp. Holotype no. 33417, ×3.6. Loc. A-8331. (p. 411)
14, 15—*Keilostoma quaidei* Allison, n. sp. Holotype no. 33452, ×2.0. Loc. A-8321. (p. 414)
16—*Neritoma* (*Neridomus*) *woodfordi* Allison, n. sp. Holotype no. 33429, ×2.0. Loc. A-8331. (p. 413)
17—*Turritella? durhami* Allison, n. sp. Holotype no. 33462, ×4.4. Loc. A-8331. (p. 415)
18—*Semineritina apparata* (Cragin). Hypotype no. 33410, ×8.0. Loc. A-8317. (p. 414)
19—*Encycloscala emersoni* Allison, n. sp. Paratype no. 33419, ×3.6. Loc. A-8331. (p. 411)
20—*Cirsochilus gilberti* Allison, n. sp. Holotype no. 33425, ×4.8. Loc. A-8317. (p. 411)



Allison, Middle Cretaceous Gastropoda, Baja California



Allison, Middle Cretaceous Gastropoda, Baja California

MICROSCHIZA (CLOUGHTONIA) SCALARIS
(Conrad)
Pl. 41, figs. 1, 2

Natica? scalaris CONRAD, 1852, in Lynch, W. F., U. S. Exped. to explore the Dead Sea and River Jordan, Append., p. 234, pl. 7, fig. 50.
Coronatica purpuroidea BLANCKENHORN, 1927, Palaeontographica, Band 69, p. 135, pl. 2, figs. 26a–c.
Microschiza (Cloughtonia) scalaris (Conrad). DELPEY, 1939, Notes et Mém. Soc. d'Études Géol. Haut. Comm. Rép. Française en Syrie et au Liban, tome 3 (1940), pp. 70–71, text figs. 44–45.

Hypotypes.—Nos. 33427 (fig. 1) and 33428 (fig. 2), loc. A-8331.

Occurrence.—Punta China, loc. A-8331 (F).

Remarks.—This species has been reported from various Mediterranean localities in strata assigned ages ranging from upper Aptian to lower Cenomanian.

Superfamily NERITACEA
Family NERITIDAE
Subfamily NERITINAE
Genus NERITOMA Morris

Neritoma MORRIS, 1849, Quart. Jour. Geol. Soc. London, vol. 5, p. 332.

Type species (Cossman, 1925, fide Wenz, 1938): *Nerita sinuosa* Sowerby.

Subgenus NERIDOMUS Morris & Lycett

Neridomus MORRIS & LYCETT, 1851, Palaeontogr. Soc. Monogr. no. 1, p. 77.

Type species: *Nerita hemisphaerica* Morris and Lycett.

NERITOMA (NERIDOMUS) WOODFORDI
Allison, n. sp.
Pl 40, fig. 16

Shell moderately large, heavy, low-spired; sutures indistinct; body whorl very large with slightly concave posterior surface profile; inner lip of aperture heavily callused; apertural margin of callus nearly straight, smooth; outer margin of callus straight, parallel to apertural margin at an angle of 35° with axis of shell; callus area squarely truncated anteriorly; shell surface smooth except for growth lines.

Holotype.—No. 33429, loc. A-8316.

Dimensions.—Holotype: height 21.7 mm., diameter about 20 mm., apical angle very large.

Occurrence.—Punta China, loc. A-8316 (R).

Remarks.—This species closely resembles *"Nerita" taramellii* Pirona (1883, p. 9, pl. 1 fig. 10) as figured by Parona (1909, pl. 24, figs, 1a–b, 3, 4) from the "Cenomanian" of Italy. The Italian species, however, appears to have a narrower aperture. The figured specimens of *"Nerita" taramellii* show a sinuous outer callus margin distinguishing it from the Baja California species. Only one specimen of *Neritoma (Neridomus) woodfordi* is now available so that variation in this character cannot be evaluated. Examination of suites of recent specimens closely related to this genus has failed to reveal sufficient variation in the linearity or sinuosity of the outer callus margin to justify reference of this specimen to Pirona's species.

NERITOMA (NERIDOMUS) DELPEYAE
Allison, n. sp.
Pl. 40, figs. 9, 10

Shell very small, low spired, with very large and globose body whorl; volutions three or four; sutures distinct; whorls ornamented by very fine growth lines only; aperture large, semilunate in outline; inner lip with heavy, parallel sided callus, outer callus margin convergent with apertural margin anteriorly.

EXPLANATION OF PLATE 41

FIGS. *1, 2*—*Microschiza (Cloughtonia) scalaris* (Conrad). *1*, Hypotype no. 33427, ×0.8, *2*, Hypotype no. 33428, ×0.8. Loc. A-8331. (p. 413)
3—*Mesalia (Mesalia) mauryae* Allison, n. sp. Holotype no. 33454, ×3.6. Loc. A-8331. (p. 414)
4—*Cimolithium miyakoense* (Nagao). Hypotype no. 33531, ×1.1. Loc. A-8321. (p. 418)
5—*Turritella (Haustator)* aff. *T. (H.) seriatimgranulata* Roemer. Hypotype no. 33461, ×1.9. A-8331. (p. 415)
6—*Cassiope (Cassiope) kleinpelli* Allison, n. sp. Holotype no. 33467, ×1.1. Loc. A-8331. (p. 416)
7—*Cassiope (Gymnentome) gwynae* Allison, n. sp. Holotype no. 33473, ×1.0. Loc. A-8331. (p. 416)

Holotype.—No. 33430, loc. A-8317.

Dimensions.—Holotype: height 4.8 mm., diameter 3.6 mm., apical angle greater than 90°.

Occurrence.—Punta China, loc. A-8317 (R).

Remarks.—This small species is distinguished from such related species as *N.* (*N.*) *woodfordi* n. sp. and "*Nerita* (*Ampullina*)" *minima* Whitfield (1891, pp. 418–419, pl. 8, figs. 5–6) by its small size, short spire, and apertural characteristics.

Genus OTOSTOMA d'Archiac

Otostoma D'ARCHIAC, 1856, Bull. Soc. Géol. France, ser. 2, tome 16, p. 871.

Type species: *Otostoma ponticum* d'Archiac.

Subgenus LYOSOMA White

Lyosoma WHITE, 1883, U. S. Geol. Survey Territories Ann. Rept., vol. 12, p. 152.

Type species: *Neritina? powelli* White.

OTOSTOMA (LYOSOMA) JAPONICA (Nagao)
Pl. 40, figs. 11, 12

Desmieria japonica NAGAO, 1934, Jour. Faculty Sci., Hokkaido Imp. Univ., ser. 4, vol. 2, no. 3, pp. 237–238, pl. 36, figs. 19, (?) 20, 21–23.

Hypotype.—No. 33409, loc. A-8317.

Occurrence.—Punta China, loc. A-8317 (C).

Remarks.—This species occurs in the Miyako District, Honshu, Japan, in the Hiraiga sandstone (type locality) and Akito sandstone. The age of these beds may be upper Aptian or Albian.

Genus SEMINERITINA Cossmann

Semineritina COSSMANN, 1925, Essais Paléonch., tome 13, p. 215.

Type species: *Nerita mammaria* Lamarck.

SEMINERITINA APPARATA (Cragin)
Pl. 40, fig. 18

Neritina apparata CRAGIN, 1893, Texas Geol. Survey Ann. Rept. no. 4, p. 227, pl. 46, fig. 14; ——, ADKINS, 1928, Univ. Texas Bull. 2838, p. 174.

Nerita? apparata (Cragin). STANTON, 1947, U. S. Geol. Survey Prof. Paper 211, p. 61, pl. 47, figs. 14, 15.

Hypotype.—No. 33410, loc. A-8317.

Occurrence.—Punta China, loc. A-8317 (F).

Remarks.—This species occurs in the Edwards limestone (middle Albian), Howard (type locality) and Travis Counties, Texas.

Order MESOGASTROPODA
Superfamily RISSOACEA
Family RISSOIDAE
Subfamily RISSOINAE
Genus KEILOSTOMA Deshayes

Keilostoma DESHAYES, 1850, Traité Élém. Conch., Atlas, p. 46.

Type species: *Bulimus turricula* Bruguière.

KEILOSTOMA QUAIDEI Allison, n. sp.
Pl. 40, figs. 14, 15

Shell moderately small, high-spired smooth; volutions about nine, slightly convex in profile, sutures only slightly impressed; aperture ovate, holostomate; outer lip greatly thickened; inner lip callused; imperforate.

Holotype.—No. 33452, loc. A-8321. Paratype: no. 33482, loc. A-8321.

Dimensions.—Holotype: height (incomplete) 19.0 mm., diameter about 8.0 mm., apical angle 30°.

Occurrence.—Punta China, loc. A-8321 (R).

Remarks.—This species closely resembles *Keilostoma subulatum* Stoliczka (1868, p. 282, pl. 20, figs. 21a–c) from the Arrioloor group near Arrioloor, southern India. *K. subulatum* has a similar profile and also lacks surface ornamentation but its apertural thickening is much wider than that on *K. quaidei*.

Superfamily CERITHIACEA
Family TURRITELLIDAE
Genus MESALIA Gray

Mesalia GRAY, 1842, Syn. Cont. British Mus., ed. 1842, p. 147.

Type species (Gray, 1847, fide Wenz, 1939): *Cerithium mesal* Adanson.

Subgenus MESALIA s. s.

MESALIA (MESALIA) MAURYAE Allison, n. sp.
Pl. 41, fig. 3

Shell small, high-spired; volutions 8–10, slightly convex in profile, sutures deeply

impressed; whorl sculpturing of four approximately equal spiral ribs, interspaces about same width; a fifth spiral rib sometimes apparent on later whorls, occasionally comparable in strength to four primary ribs; base of body whorl with similar spiral ribs; aperture entire, anterior canal rudimentary.

Holotype.—No. 33454, loc. A-8331. Paratypes: nos. 33455, 33456, 33458–33460, loc. A-8331.

Dimensions.—Holotype: height (very incomplete) 10.2 mm., diameter at least 4 mm., apical angle 20–25°.

Occurrence.—Punta China, loc. A-8331 (C).

Remarks.—The spiral ornamentation which characterizes this species is known also on several other Cretaceous species. *Mesalia hebe* White, from Brazil, probably of middle Albian age, is similar to *M.* (*M.*) *mauryae* but carries five spiral ribs on adult whorls. Adult specimens of the Brazilian species are about twice the size of the Baja California specimens, all of which are the size of the holotype or smaller. *M.* (*M.*) *mauryae* therefore appears to be a smaller species than *M. hebe*, the latter being characterized by a well developed fifth spiral rib.

Genus TURRITELLA Lamarck

Turritella LAMARCK, 1799, Mém. Soc. Nat. Paris, ser. 1, tome 1, p. 74.

Type species: *Turbo terebra* Linnaeus.

Subgenus HAUSTATOR Montfort.

Haustator MONTFORT, 1810, Conch. Syst., tome 2, p. 182.

Type species: *Haustator gallicus* Montfort.

TURRITELLA (HAUSTATOR) aff. T. (H.) SERIATIMGRANULATA Roemer

Pl. 41, fig. 5

Turritella seriatimgranulata Roemer. STANTON, 1947, U. S. Geol. Survey Prof. Paper 211, pp. 75–76, pl. 56, figs. 17, 24.

Hypotype.—No. 33461, loc. A-8331.

Occurrences.—Punta China, loc. A-8331 (A) and loc. A-8332 (A).

Remarks.—The uniformity in ornamentation exhibited by the very abundant Punta China specimens as compared with specimens recorded in the literature as belonging to this species suggests that several taxonomic entities of at least subspecific rank have been grouped indiscriminately under the name *Turritella seriatimgranulata*. The Punta China specimens most closely resemble those from the "Potrero" formation near Arivechi, Sonora,[1] to which King (1939, pp. 1670–1671) referred as "*Turritella* aff. *seriatim-granulata*."

Turritella (*Haustator*) *seriatimgranulata* Roemer sensu lato is recorded from strata of middle Albian and perhaps lower Albian ages.

TURRITELLA? DURHAMI Allison, n. sp.

Pl. 40, fig. 17

Shell small, high-spired; volutions 8–10 each with diameter about twice height; whorl profile straight except for posterior and anterior ribbon-like constrictions, each equal to about one-fourth height of whorl; sutures slightly impressed, bordered posteriorly by subdued cord; whorl surface with about 35 very fine spiral ribs; ribs irregularly spaced, increasingly crowded towards anterior suture; shell sharply angled anteriorly; base with low spiral carina near periphery and 30–40 very fine ribs, wider towards umbilicus; aperture low, entire.

Holotype.—No. 33462, loc. A-8331. Paratype: no. 33466, loc. A-8331.

Dimensions.—Holotype: height (incomplete, three youngest whorls) 4.8 mm., diameter 4.4 mm., apical angle about 30°.

Occurrence.—Punta China, loc. A-8331 (F).

Remarks.—This distinctive little gastropod is difficult to assign generically. *Turritella sylviana* Hyatt, 1870, as figured by White (1888, pl. 18, fig. 10) from the Cretaceous of Brazil is similar to the Punta China species in gross aspect. Hyatt's species, however, appears to lack the two ribbon-like constrictions on each whorl. Cossmann (1912, tome 9, p. 117) places the Brazilian species in the subgenus *Haustator* but this does not appear to be justified.

[1] The name "Potrero" formation is preoccupied by a Lower Jurassic marine shale formation of southeastern Mexico (Böse, 1898, p. 175), as pointed out by Imlay (1944, p. 1036).

Family THIARIDAE
Subfamily MELANOPSINAE
Genus CASSIOPE Coquand

Cassiope COQUAND, 1865, Mém. Soc. Emul. Provence, tome 3, p. 247.

Type species: *Turritella kefersteini* Goldfuss.

Subgenus CASSIOPE s. s.
CASSIOPE (CASSIOPE) KLEINPELLI
Allison, n. sp.
Pl. 41, fig. 6

Shell of moderate size, high-spired, straight-sided; volutions about ten, generally straight-sided; sutures slightly impressed; adult whorl ornamentation of two well developed, slightly noded, spiral primary ribs; upper primary rib slightly posterior from whorl center on later whorls, still more posterior on juvenile whorls; anterior primary rib borders suture, increasingly sharp and smooth on earlier whorls; earlier whorls with secondary spiral ornamentation of slightly raised lines alternating with finer tertiary raised lines; three such secondary lines between two primary ribs, several more posteriorly except on earliest whorls where secondary ornamentation dominates; rounded base of body whorl with two noded spiral ribs slightly weaker than primary ribs of side of whorl; several additional faintly raised lines between the two noded spiral ribs and the umbilical region; umbilicus closed; aperture holostomate, semi-ovate in outline; pigmentation pattern probably dark spiral primary ribs with lighter intervening areas.

Holotype.—No. 33467, loc. A-8331. Paratypes: nos. 33468–33472, loc. A-8331.

Dimensions.—Holotype: height (almost complete) 41.1 mm., diameter 19.9 mm., apical angle 25° to 30°.

Occurrence.—Punta China, loc. A-8331 (A).

Remarks.—The uniformity exhibited by over fifty specimens from Punta China eliminates the possibility of assigning this species to any of the previously described species reported from the Americas, Asia, or the Mediterranean region. "*Glauconia strombiformis* (Schlotheim)" figured by Delpey (1939, text-fig. 73, pl. 5, fig. 4) from North Africa has similarly arranged spiral ornamentation but has a lower spire than *C.* (*C.*) *kleinpelli* n. sp. Likewise, some of the specimens figured by Rehbinder (1902, pl. 2, figs. 1–3 *only*) and referred to Schlotheim's species, are closely related to *C.* (*C.*) *kleinpelli* n. sp. but differ in their much more pronounced secondary spiral ornamentation. Specimens from Utrillas, northeastern Spain, referred to Schlotheim's species by Verneuil and Lorière (1868, pl. 1, figs. 4 and 4e) differ from the Punta China species in their less elevated profiles and slight separation of anterior primary ribs from adjacent sutures. "*Paraglauconia*" *sergipensis* Maury (1936, pp. 208–211, pl. 12, fig. 9) has a higher spire and more convex whorl profile.

The interrelationships of these and numerous species of *Cassiope* s. s. can be determined only after the adequacy of many illustrations and descriptions is checked against actual specimens. Distinct taxonomic units have apparently been frequently grouped under a single name. Certainly the amount of variation indicated by illustrations of fossils referred to Schlotheim's species, *Glauconia strombiformis*, would far surpass the amount of variation exhibited by the closely related *Cassiope* (*Cassiope*) *kleinpelli* n. sp.

Subgenus GYMNENTOME Cossmann

Gymnentome COSSMANN, 1909, Essais Paléonch. Comp., tome 8, p. 169.

Type species: *Turritella renauxiana* d'Orbigny.

CASSIOPE (GYMNENTOME) GWYNAE
Allison, n. sp.
Pl. 41, fig. 7

Shell large, smooth, high-spired; spire profile slightly convex in early portion; volutions about 11; early whorls slightly convex in profile, latest whorls often slightly concave; earliest four or five whorls with two sharp spiral carinae dividing whorls approximately evenly; anterior carina much more strongly developed at first giving whorl profile sharply angled appearance; two carinae almost equally developed on whorls five and six, both obsolete on later whorls; fine supplementary spiral ornamentation apparent on earliest whorls; anterior extremity of whorls with low cord exposed

at suture, increasingly widely separated from suture on latest whorls; body whorl with two spiral ribs, the posterior corresponding to anterior cord of preceeding whorls; base of body whorl without distinct spiral ornamentation; aperture ovate, with flaring lip; growth lines distinct, sinuous, with well marked sinus about one-third of whorl height from anterior suture; sinus nearer whorl midpoint on latest whorl where anterior cord separates from suture.

Holotype.—No. 33473, loc. A-8331. Paratypes: nos. 33474, 33475, loc. A-8331.

Dimensions.—Holotype: height (almost complete) 86.5 mm., diameter about 27 mm., apical angle 20° to 30°. Holotype is approximately average size.

Occurrence.—Punta China, loc. A-8331 (A).

Remarks.—*Cassiope* (*Gymnentome*) *gwynae* n. sp. appears to be more closely related to "*Glauconia* aff. *Renauxiana* d'Orbigny" as figured by Rehbinder (1902, pl. 2, figs. 8-9 *only*) than to other species noted in the literature. Rehbinder's specimens, from the Cretaceous of the Caspian region of Russia, might prove to be conspecific with the Baja California species when a more adequate comparison is possible. These specimens are very different from d'Orbigny's figures of "*Turritella*" *renauxiana* from the Turonian of Southern France, both in general shape and in nature of growth line. *Cassiope paluxiensis* Stanton (1947, pp. 78–79, pl. 57, figs. 18, 19) from the Glen Rose limestone of Texas (Albian) differs from the Baja California species in the nature and disposition of its spiral ornamentation and growth line sinus.

Family OMALAXIDAE
Genus OMALAXIS Deshayes

Omalaxis DESHAYES, 1830, Ency. Méth. (Vers.), tome 3, p. 659.

Type species: *Solarium bifrons* Deshayes.

OMALAXIS PLANORBIS (Roemer) ?

Hypotype.—No. 33788, loc. A-8317.

Occurrence.—Punta China, loc. A-8317 (R).

Remarks.—A single poorly preserved specimen of a thin planispirally coiled gastropod from Punta China resembles specimens from the Edwards limestone and Fredricksburg group of Texas referred to Roemer's species, *Omalaxis planorbis* (Stanton, 1947, p. 64, pl. 55, figs. 23–26). Without additional and more perfectly preserved material a more definite identification is impossible.

Family PROCERITHIIDAE
Subfamily METACERITHIINAE
Genus METACERITHIUM Cossmann

Metacerithium COSSMANN, 1906, Essais Paléoconch. Comp., tome 7, p. 54.

Type species: *Cerithium trimonile* Michelin.

METACERITHIUM sp.
Pl. 42, fig. 7

Hypotype.—No. 33486, loc. A-8331.

Occurrence.—Punta China, loc. A-8331 (F).

Remarks.—The studied section at Punta China has thus far produced only several very incomplete representatives of this species. Inland, however, specimens in a finer state of preservation occur fairly commonly but, because of their uncertain stratigraphic relationship to the specimens from locality A-8331, their description will have to await further study.

Specimens of *Metacerithium* from the Alisitos formation closely resemble *Metacerithium trimonile* (Michelin), the type species of the genus, as figured by Cossmann (1906, tome 7, pl. 6, fig. 30). Michelin's species, from the Albian of Europe, has less prominent noded spiral ribs than the Alisitos species.

Genus UCHAUXIA Cossmann

Uchauxia COSSMANN, 1906, Essais Paléoconch. Comp., tome 7, pp. 56–57.

Type species: *Cerithium peregrinorsa* d'Orbigny.

UCHAUXIA KIRKI Allison, n. sp.
Pl. 42, fig. 3

Shell small, turreted, high-spired; general spire profile slightly convex; volutions about 12, straight-sided; whorl sides parallel to axis of spire giving profile shouldered appearance, each whorl sharply truncated posteriorly at impressed suture; whorl ornamentation of three equally spaced spiral primary ribs alternating with three secondary

ribs, several additional very fine raised lines in excavated sutural area; nodes produced by juncture of spiral ribs with about 25 axial ribs; axial ribs somewhat irregularly spaced, about equal in width to interspaces; nodes of posterior primary rib directed outward and slightly posteriorly over sutural area; ornamentation of earliest whorls similar but with fewer axial ribs and with three main spiral ribs only; base of body whorl rounded, imperforate, smooth except for subdued spiral ribs near periphery, inner lip of aperture produced anteriorly from columella; anterior canal short, narrow.

Holotype.—No. 33487, loc. A-8321. Paratypes: nos. 33488–33490, 33494, loc. A-8317; 33495, 33496, 33498–33500, 33506, loc. A-8321.

Dimensions.—Holotype: height (almost complete) 20.0 mm., diameter 5.6 mm., apical angle 25° to 30°.

Occurrences.—Punta China, locs. A-8317 (C) and A-8321 (C).

Remarks.—This species resembles "*Cerithium*" *quitmanense* Stanton (1947, pp. 100–101, pl. 64, figs. 12, 17) from the Fredericksburg group of Texas. The Texas species, however, has a higher and straighter profile and lacks the distinctive shouldered appearance of *Uchauxia kirki* n. sp.

Uchauxia beali Allison, n. sp.
Pl. 42, fig. 8

Shell similar in general shape to type of genus; volutions about 15; sutures very slightly impressed; anterior canal probably short, narrow, slightly curved; whorl ornamentation of about six irregular axial ribs extending from suture on early portion of spire, broken into progressively more pronounced nodes on later portion with increasingly prominent spiral discipline; three such rows of spiral nodes on latest three or four whorls, four rows present earlier; second row of nodes from posterior suture best developed, second row from anterior suture weakest, disappearing completely on latest whorls; 20 to 30 secondary spiral ribs on entire whorl surface, about equal in width to interspaces; especially well developed between three or four main rows of nodes base of body whorl with faint traces of spiral ornamentation.

Holotype.—No. 33507, loc. A-8321. Paratypes: nos. 33508, 33512, 3315–33517, 33526, loc. A-8317; 33527–33530, loc. A-8321.

Dimensions.—Holotype: height (almost complete) 26.8 mm., diameter 9.4 mm., apical angle about 26°.

Occurrences.—Punta China, loc. A-8317 (C) and A-8321 (C).

Remarks.—This species in shape and ornamentation resembles "*Cerithium*" *chirsophorum* Parona (1909, p. 226, pl. 26, figs 28, 29a–b) from the "Cenomanian" of Italy, particularly his figures 29a and b. However, the incompletnesss of Parona's material makes determination of exact relationships impossible.

Genus Cimolithium Cossmann

Cimolithium Cossmann, 1906, Essais Paléoconch. Comp., tome 7, pp. 57–58.

Type species: *Cerithium belgicum* d'Archiac.

Cimolithium miyakoense (Nagao)
Pl. 41, fig. 4; Pl. 42, fig. 6

Cerithium (*Cimocerithium* ?) *miyakoense* Nagao, 1934, Jour. Faculty Sci., Hokkaido Imp. Univ., ser. 4, vol. 2, no. 3, pp. 252–255, pl. 36, figs. 1–10.

Hypotypes.—Nos. 33531 (Pl. 41, fig. 4), 33532 (Pl. 42, fig. 6), 33536, loc. A-8321.

Occurrences.—Punta China, locs. A-8317 (C) and A-8321 (C).

Remarks.—This species occurs in the Hiraiga sandstone and the Akito sandstone of the Miyako District, Honshu, Japan. The sequence which includes these two stratigraphic units ranges in age from upper Aptian to Gault, according to Yabe and Hanzawa (1926, p. 20) with all but the very uppermost beds probably older than Gault.

Specimens from Punta China are about equal in size to those figured by Nagao, although specimens are occasionally encountered which attain about twice that size. Little can be added to the original description except that the pattern of pigmentation exhibited by several of the Punta China specimens consists of a series of spots and streaks about equal in density to the nodose ornamentation and largely concentrated on the anterior two-thirds of each whorl (Pl. 42, fig. 6). The spots are arranged in three or four irregular spiral rows with

spots of adjacent rows occasionally joined by oblique streaks.

CIMOLITHIUM MIYAKOENSE (Nagao) var. TOMÁSENSIS Allison, n. var.
Pl. 42, fig. 2

Among the specimens of *C. miyakoense* s. s. collected at Punta China locality A-8317 are several turreted specimens characterized by dominant axial ribs, slightly offset anteriorly, instead of by anterior and posterior spiral rows of nodes. Slight traces of pigmentation are apparent on the holotype of this variety but the pattern is too indistinct for comparison with *C. miyakoense* s. s.

Holotype.—No. 33533, loc. A-8317. Paratype no. 33534, loc. A-8317.

Dimensions.—Holotype: height (incomplete) 26.3 mm., diameter 12.3 mm., apical angle about 27°.

Occurrence.—Punta China, loc. A-8317 (F).

CIMOLITHIUM ELEANORAE Allison, n. sp.
Pl. 42, fig. 4

Shell moderately small, high-spired, turreted; spire profile slightly inflated; volutions about 11, slightly convex with greater diameter just anterior of whorl center; whorl profile dominated by posterior noded cord bordering suture; nodes of cord about 28 in number on adult whorls, half that many posteriorly curved thin axial ribs extend from nodes to anterior suture; entire whorl surface with about fifty low, often indistinct, flat-topped spiral ribs, about twice the width of interspaces; axial ribs obsolete on late whorls of some specimens; body whorl angulated anteriorly; base smooth; anterior canal moderately long, straight.

Holotype.—No. 33537, loc. A-8321. Paratypes: nos. 33544–33547, loc. A-8317.

Dimensions.—Holotype: height (almost complete) 26.5 mm., diameter 19.7 mm., apical angle about 26°.

Occurrences.—Punta China, locs. A-8317 (C) and A-8321 (F).

Remarks.—This species is closely related to *"Cerithium" bushwackense* Irkins and Clabauch (1940, p. 14, pl. 2, figs. 5a–b) from the Edwards formation of Texas (middle Albian). The Texas species, however, has two anterior spiral rows of nodes instead of one and has much heavier axial ribs on the adult whorls.

Family POTAMIDIDAE
Subfamily POTOMIDINAE
Genus PYRAZUS Montfort

Pyrazus MONTFORT, 1810, Conch. Syst., tome 2, p. 458.

Type species: *Cerithium boudini* Montfort

Sugeus ECHINOBATHRA Cossmann

Echinobathra COSSMANN, 1906, Essais Paléoconch. Comp., tome 7, pp. 131–132.

Type species: *Cerithium simonyi* Zekeli.

PYRAZUS (ECHINOBATHRA) AUSTINENSE (Roemer)
Pl. 42, figs. 9, 10

Cerithium austinense ROEMER, 1888, Palaeont. Abh., Band 4, p. 16, (294), pl. 1 (31), fig. 12; ——, STANTON, 1947, U. S. Geol. Survey Prof. Paper 211, pp. 96–97, pl. 64, fig. 29.
Cerithium? austinense Roemer. ADKINS, 1928, Texas Univ. Bull. 2838, p. 188.

Hypotypes.—Nos. 33549 (fig. 9) and 33548 (fig. 10), loc. A-8317.

Occurrence.—Punta China, loc. A-8317 (F).

Remarks.—This species occurs in the Edwards limestone (middle Albian) of Travis County, Texas. The Punta China specimens are, in general, about twice as large as the Texas specimens figured by Stanton (1947, pl. 64, fig. 29) and those in the collection of the University of California (15 to 20 mm. long).

PYRAZUS (ECHINOBATHRA) DURHAMI Allison, n. sp.
Pl. 42, fig. 12

Shell small, very high-spired, straight-sided; volutions at least 11; whorls strongly convex in profile, diameter about twice height; sutures distinct, anterior to narrowest part of whorl, at approximately 92° angle to spire axis; growth line with moderately strong sinus; adult whorl ornamentation of eight or nine short, strong axial ribs plus densely spaced spiral ribs over entire whorl surface; axial ribs not aligned on successive whorls, about half the width of adjacent interspaces, sharply terminated posteriorly at suture, more gently subdued anteriorly just beyond midpoint of whorl;

prominent basal keel indicated by broad constricted area between anterior ends of axial ribs and inflated anterior margin of whorl; six primary spiral ribs located over portion of whorl where axial ribs developed, approximately equally spaced, slightly nodose where crossed by growth lines; primary ribs alternate with secondary and tertiary ribs, the latter becoming progressively finer anteriorly across whorl constriction toward suture; nature of body whorl unknown.

Holotype.—No 33539, loc. A-8317. Paratypes: nos. 33550, 33554, 33555, loc. A-8321; nos. 33558–33560, loc. A-8331.

Dimensions.—Holotype: height (incomplete) 16.4 mm., diameter 6.8 mm., apical angle 7°.

Occurrences.—Punta China, locs. A-8317 (R), A-8321 (C), A-8331 (F).

Remarks.—The body whorl and aperture of this species are unknown. The spire, however, vaguely resembles that of *Cerithium problematicum* Zekeli (see Cossmann, 1906, tome 7, pl. 14, fig. 25) from the Turonian of Gosau. The European species lacks the strong basal disc of the Punta China species.

PYRAZUS? HARRISSI Allison, n. sp.
Pl. 42, fig. 1

Shell large, heavy, high-spired; volutions probably between 10 and 15; whorl ornamentation coarse, dominated by eight or nine heavy axial ribs on adult whorls; axial ribs interrupted at sutures but approximately aligned on adjacent whorls; superimposed spiral ornamentation of two heavy ribs located slightly anterior to midpoint of whorl, and at least six much lighter secondary ribs; one secondary rib between two main ribs; finer tertiary and quaternary spiral ribs alternating with more prominent ornamentation; anterior canal probably short, curved.

Holotype.—No. 33563, loc. A-8317.

Dimensions.—Holotype: height (three last whorls) 50 mm., diameter about 35 mm., apical angle about 35°.

Occurrence.—Punta China, loc. A-8317 (R).

Remarks.—This species is much larger and heavier than *Pyrazus* (*Echinobathra*) *austinense* (Roemer) with which it occurs at Punta China. The axial ribs are stronger on *Pyrazus? harrissi* n. sp. and its spiral ornamentation is distinctive. The only available specimen, the holotype, is badly beach worn and further defaced by borings (probably sponge) and by encrusting worm tubes.

Family CERITHIIDAE
Subfamily CERITHIINAE
Genus CERITHIUM Bruguière

Cerithium BRUGUIÈRE, 1789, Ency. Méth. (Vers.), tome 1, p. xv.

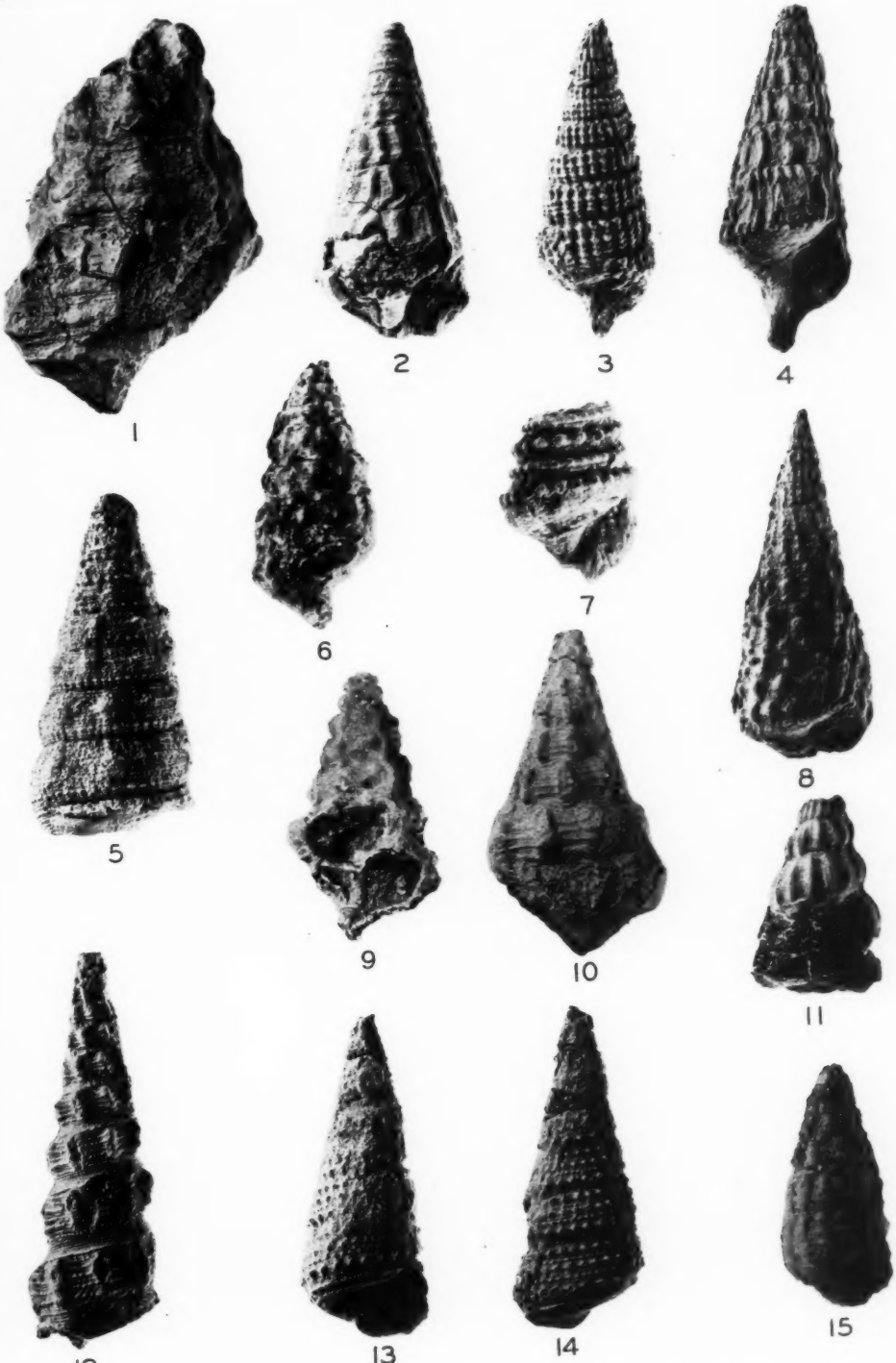
Type species: *Cerithium nodulosum* Bruguière.

CERITHIUM? EMERSONI Allison, n. sp.
Pl. 42, fig. 5

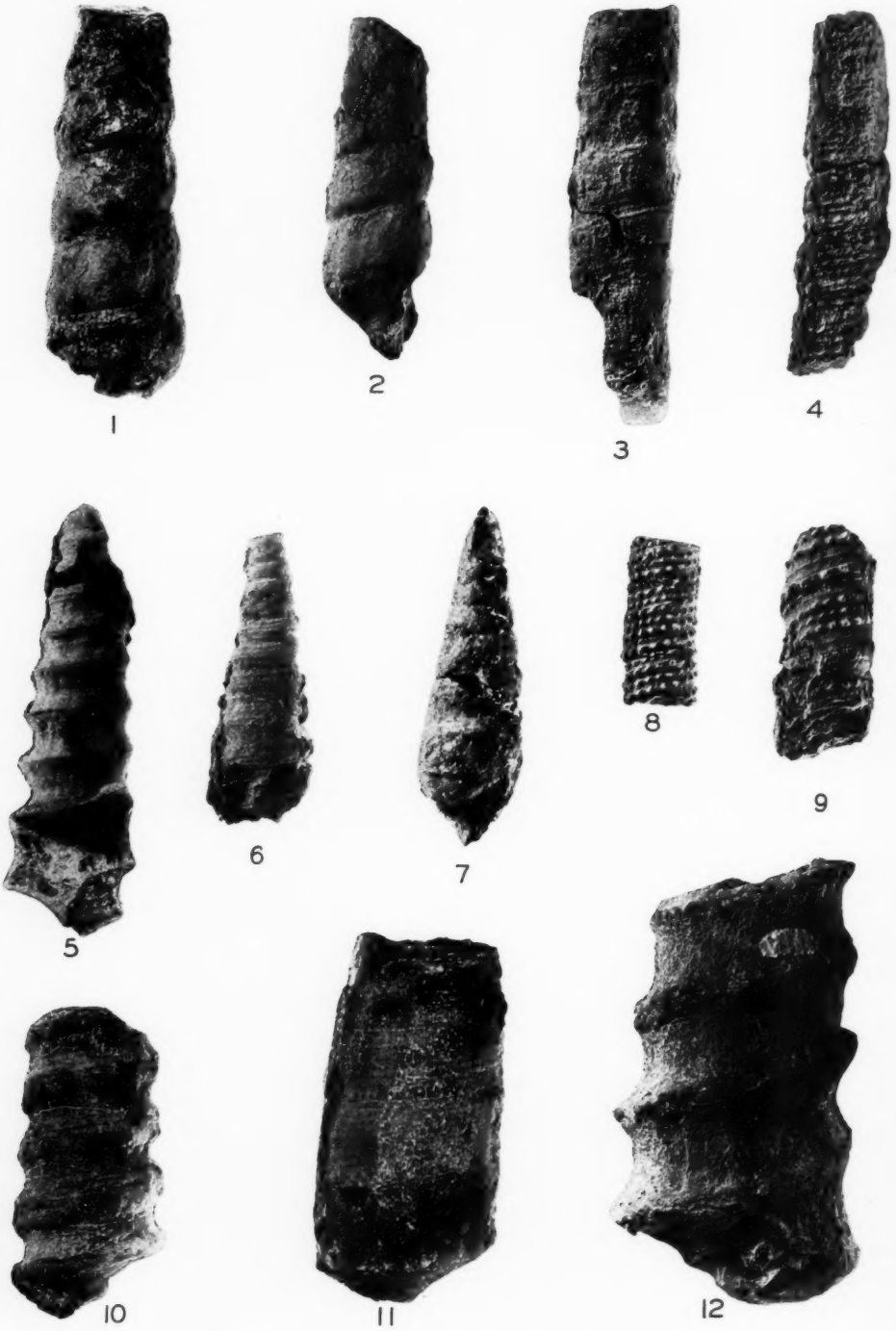
Shell of medium size, high-spired; spire profile almost straight-sided; volutions prob-

EXPLANATION OF PLATE 42

FIGS. *1*—*Pyrazus? harrissi* Allison, n. sp. Holotype no. 33563, ×1.0. Loc. A-8317. (p. 420)
2—*Cimolithium miyakoense* (Nagao) var. *tomásensis* Allison, n. var. Holotype no. 33533, ×1.6. Loc. A-8317. (p. 419)
3—*Uchauxia kirki* Allison, n. sp. Holotype no. 33487, ×2.2. Loc. A-8321. (p. 417)
4—*Cimolithium eleanorae* Allison, n. sp. Holotype no. 33537, ×1.7. Loc. A-8321. (p. 419)
5—*Cerithium? emersoni* Allison, n. sp. Holotype no. 33561, ×2.3. Loc. A-8321. (p. 420)
6—*Cimolithium miyakoense* (Nagao). Hypotype no. 33532, ×1.0. Loc. A-8321. (p. 414)
7—*Metacerithium* sp. Hypotype no. 33486, ×4.0. Loc. A-8331. (p. 417)
8—*Uchauxia beali* Allison, n. sp. Holotype no. 33507, ×1.7. Loc. A-8321. (p. 418)
9, 10—*Pyrazus* (*Echinobathra*) *austinense* (Roemer). *9*, Hypotype no. 33549, ×1.6; *10*, Hypotype no. 33548, ×2.0. Loc. A-8317. (p. 419)
11—*Amaea* (*Confusiscala*) sp. Hypotype no. 33574, ×2.5. Loc. A-8331. (p. 422)
12—*Pyrazus* (*Echinobathra*) *durhami* Allison, n. sp. Holotype no. 33539, ×3.3. Loc. A-8317. (p. 419)
13, 14—*Cerithiella* (*Cerithiella*) *kickapooense* (Stanton)?. Hypotype no. 33573, ×3.3. Loc. A-8331. (p. 422)
15—*Cerithiopsis? stantoni* Allison, n. sp. Holotype no. 33566, ×3.0. Loc. A-8321. (p. 421)



Allison, Middle Cretaceous Gastropoda, Baja California



Allison, Middle Cretaceous Gastropoda, Baja California

ably between 10 and 15, low, inflated, with angular profile; whorl diameter about three times height; adult spiral ornamentation of eight or nine axial ribs, much subdued toward sutures; superimposed spiral ornamentation of two primary ribs, three secondary ribs, about 11 tertiary ribs, and an undetermined number of quaternary ribs; one noded primary rib near anterior suture of whorl, other primary at summit of axial ribs (slightly posterior of whorl center), less nodose; a secondary rib between two primary ribs (thus slightly anterior of whorl center), pair of closely spaced secondary ribs bordering posterior suture and separated by at least three tertiary ribs between secondary rib just anterior of whorl center and posterior primary rib, three tertiary ribs between posterior primary rib and posterior pair of secondary ribs; an indeterminate number of quaternary ribs alternating with the stronger spiral ribs of whorl; body whorl and nature of aperture unknown.

Holotype.—No. 33561, loc. A-8321.

Dimensions.—Holotype: height (incomplete) 18.0 mm., diameter 9.0 mm., apical angle about 20°.

Occurrence.—Punta China, loc. A-8321 (R).

Remarks.—The single available specimen of *Cerithium? emersoni* n. sp. is incomplete, lacking both earliest and latest whorls. This generic assignment is therefore based merely on the general shape of the spire and on the character of its ornamentation. In these aspects the species resembles *C. vulgatum*, the type species of the subgenus *Thericium;* the chief differences being a slightly lower whorl profile and a reduced number of axial ribs on the Baja California species.

Family CERITHIOPSIDAE
Genus CERITHIOPSIS Forbes & Hanley

Cerithiopsis FORBES & HANLEY, 1851, Hist. British Moll., vol. 3, p. 364.

Type species (by monotypy): *Murex tubercularis* Montague.

CERITHIOPSIS? STANTONI Allison, n. sp.
Pl. 42, fig. 15

Shell small, moderately high-spired; spire profile slightly inflated; volutions eight or nine, diameter about twice height, convex in profile; about 12 massive axial ribs with rounded interspaces of similar width, not aligned on successive whorls, gradually subdued anteriorly toward suture, abruptly truncated posteriorly at suture, giving suture sinuous appearance; superimposed spiral ornamentation of six or seven primary ribs alternating with finer raised lines; base of body whorl imperforate, smooth except for faint traces of spiral ribs near periphery; anterior canal probably short, curved.

Holotype.—No. 33566, loc. A-8321. Paratypes: nos. 33567–33569, loc. A-8321.

Dimensions.—Holotype: height (almost complete) 11.2 mm., diameter 5.0 mm., apical angle about 25°.

Occurrence.—Punta China, loc. A-8321 (C).

Remarks.—The well developed axial ribs and a lack of complete apertural data on available specimens obscure the generic relationships of this species. *Cerithiopsis* (*Cerithiopsis*) *tubercularis* (Montague), the

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EXPLANATION TO PLATE 43

FIGS. *1, 2*—*Pseudonerinea stirtoni* Allison, n. sp. *1*, Paratype no. 33589, ×1.3; *2*, Holotype no. 33587, ×1.1. Loc. A-8332. (p. 423)

3, 4—*Aptyxiella* (*Aptyxiella*) cf. *A.* (*A.*) *subula* (Roemer). *3*, Hypotype no. 33712, ×3.3, Loc. A-8317; *4*, Hypotype no. 33713, ×4.2, Loc. A-8321. (p. 425)

5, 6—*Nerinea* (*Plesioptygmatis*) cf. *N.* (*P.*) *pseudoconvexa* Stanton. *5*, Hypotype no. 33591, ×2.3; *6*, Hypotype no. 33603, ×2.2. Loc. A-8317. (p. 423)

7—*Pseudonerinea stantoni* Allison, n. sp. Holotype no. 33578, ×5.2. Loc. A-8331. (p. 423)

8, 9—*Aptyxiella* (*Endiatrachelus*) *parallela* (Anderson and Hanna). *8*, Hypotype no. 33715, ×2.9, Loc. A-8331; *9*, Hypotype no. 33714, ×3.3, Loc. A-8321. (p. 426)

10—*Nerinea* (*Plesioptygmatis*) *tomásensis* Allison, n. sp. Paratype no. 33766, ×1.1. Loc. A-8313. (p. 425)

11—*Nerinea* (*Plesioptygmatis*) *bösei* Allison, n. sp. Holotype no. 33621, ×2.1. Loc. A-8321. (p. 423)

12—*Nerinea* (*Plesioptygmatis*) *tomásensis* Allison, n. sp. Holotype no. 33614, ×0.8. Loc. A-8313. (p. 425)

type species of the genus *Cerithiopsis*, exhibits a similar whorl profile and ornamentation density but differs significantly from *Cerithiopsis* (?) *stantoni* n. sp. in the approximately equal strength of its axial and spiral ribs. *C.* (?) *stantoni* may have a slightly curved anterior canal which, if verified by more perfectly preserved specimens, may provide an additional distinction. The anterior canal of *Ceritiopsis* s. s. is straight.

Genus CERITHIELLA Verrill

Cerithiella VERRILL, 1882, Trans. Connecticut Acad. Arts and Sci., vol. 5, p. 522.

Type species: *Cerithium metula* Lovén.

Subgenus CERITHIELLA s. s.

CERITHIELLA (CERITHIELLA) KICKAPOOENSE (Stanton)?
Pl. 42, figs. 13, 14

[?] *Cerithium kickapooense* STANTON, 1947, U. S. Geol. Survey Prof. Paper 211, p. 100, pl. 64, figs. 9–11.

Hypotype.—No. 33573, loc. A-8331.

Occurrence.—Punta China, loc. A-8331 (C).

Remarks.—Specimens occur at Punta China which in ornamentation and in general form resemble Stanton's species from the middle Albian of Texas. The Punta China specimens, however, exhibit a more strongly convex whorl profile and a less abrupt anterior termination suggesting a possible specific distinction.

Superfamily EPITONIDACEA
Family EPITONIIDAE
Genus AMAEA H. & A. Adams

Amaea H. & A. ADAMS, 1853, Genera of Recent Mollusca, vol. 1, p. 223.

Type species: *Scalaria magnifica* Sowerby.

Subgenus CONFUSISCALA de Boury

Confusiscala DE BOURY, 1909, Jour. Conch., tome 57, p. 256.

Type species: *Scalaria dupiniana* d'Orbigny.

AMAEA (CONFUSISCALA) sp.
Pl. 42, fig. 11

Shell small, moderately high-spired; whorl profile almost straight-sided; apical angle approximately 30°; volutions at least six, strongly convex in profile, each with diameter equal to two and a half times height; 15–20 varices on adult whorls, slightly diagonal to spire axis; remnants of outer lip thickening on two opposing sides of each whorl, approximately aligned on successive whorls, intersecting varices at angle of about 10°; whorl sides with about 20 fine, slightly uneven, spiral threads, heaviest posteriorly; distinct basal plate with 11 such spiral threads.

Hypotype.—No 33574, loc. A-8331.

Occurrence.—Punta China, loc. A-8331 (R).

Remarks.—This species is very similar to the type species of the subgenus *Confusiscala* from the Albian of Europe.

This relationship is not well illustrated by the single incomplete specimen (Pl. 3, fig. 11) collected from the studied section but several additional specimens from strata probably equivalent to locality A-8331, though beyond the scope of this report, show more clearly the features of the Punta China species. Spiral ornamentation of *A.* (*C.*) *dupiniana* exhibits a stronger tendency towards development of secondary spiral threads between the primary threads; a feature which is prominent only near the whorl center on Punta China specimens.

Genus OPALIA H. & A. Adams

Opalia H. & A. ADAMS, 1853, Genera of Recent Mollusca, vol. 1, p. 222.

Type species (de Boury, 1886, fide Wenz, 1940): *Scalaria australis* Lamarck.

Subgenus CRASSISCALA de Boury

Crassiscala DE BOURY, 1887, Étude Sous-genres Scalidae Bassin de Paris, p. 23.

Type species: *Scalaria francisci* Caillat.

OPALIA (CRASSISCALA) RIACHUELANUM (Maury)
Pl. 44, fig. 6

Epitonium riachuelanum MAURY, 1936, Brazil, Serv. Geol. Min., Monog., vol. 11, pp. 200–203, pl. 12, fig. 16.

Hypotype.—No. 33576, loc. A-8331.

Occurrence.—Punta China, loc. A-8331 (F).

Remarks.—The two Baja California fossils assigned to this species differ from the figure given by Maury (1936, pl. 12, fig. 16)

only in possessing a less diagonal suture. As the figure is a drawing, this apparent difference is of uncertain significance. The species occurs in Brazil in strata of middle Albian age.

Superfamily NERINEACEA
Family CERITELLIDAE
Genus PSEUDONERINEA Loriol

Pseudonerinea LORIOL in Loriol and Koby, 1890, Abh. Schweiz. Pal. Ges., bd. 17, p. 81.

Type species: *Pseudonerinea blauenensis* Loriol.

PSEUDONERINEA STANTONI Allison, n. sp.
Pl. 43, fig. 7

Shell very small, high-spired, smooth; sutures slightly impressed; volutions about 15, each with diameter more than twice height; unornamented except for slight angulation on posterior third of whorl, probably corresponding to slit band; growth line indistinct; body whorl broadly rounded anteriorly; anterior canal short, moderately narrow; nucleus weakly heterostrophous.

Holotype.—No. 33578, loc. A-8331. Paratypes: nos. 33579, 33581–33583, loc. A-8331.

Dimensions.—Holotype: height (incomplete posteriorly) 9.3 mm., diameter 2.9 mm., apical angle about 22°.

Occurrence.—Punta China, loc. A-8331 (C).

Remarks.—This species resembles *Pseudonerinea? arkansensis* Stanton (1947, p. 95, pl. 63, figs. 9–10) from the Dierks limestone of Arkansas. The Baja California species differs chiefly by its larger apical angle.

PSEUDONERINEA STIRTONI Allison, n. sp.
Pl. 43, figs. 1, 2

Shell moderately large, very high-spired, unornamented; volutions probably 20–30; profile of whorls convex, greatest diameter anterior to midpoint, diameter less than twice height; sutures impressed, steeply inclined in longitudinal section; margin of slit-band represented by fine line near posterior suture; growth line sharply deflected backwards at anterior limit of slit-band, otherwise only slightly sinuous; anterior canal short, nearly straight; nucleus not preserved on available material.

Holotype.—No. 33587 (fig. 2), loc. A-8332. Paratypes: nos. 33589 (fig. 1), 33728–33730, loc. A-8331; nos. 33721–33727, loc. A-8332.

Dimensions.—Holotype: height (four last whorls only) 42 mm., diameter 12.8 mm., apical angle between 15° and 20°.

Occurrences.—Punta China, locs. A-8331 (A) and A-8332 (A).

Remarks.—This species can be distinguished from the much smaller *Pseudonerinea stantoni* n. sp., with which it occurs, by the higher whorl profile, more numerous whorls, and less twisted anterior canal. A large number of specimens of both species is available and comparison fails to reveal an adult-juvenile relationship.

Family NERINEIDAE
Genus NERINEA Deshayes

Nerinea DESHAYES, 1827, Dict. Class. Hist. Nat., tome 11, p. 535.

Type species (by monotypy): *Nerinea mosae* Deshayes.

Subgenus PLESIOPTYGMATIS Böse

Plesioptygmatis BÖSE, 1906, Bol. Inst. Geol. Mexico, vol. 24, p. 65.

Type species (by monotypy): *Nerinea (Plesioptygmatis) burckhardti* Böse.

NERINA (PLESIOPTYGMATIS) cf. N. (P.) PSEUDOCONVEXA Stanton
Pl. 43, figs. 5, 6

Hypotypes.—Nos. 33591 (fig. 5), 33603 (fig. 6), loc. A-8317.

Occurrences.—Punta China, locs. A-8317 (F) and A-8321 (C).

Remarks. — *Nerinea (Plesioptygmatis) pseudoconvexa* Stanton has been reported from the Edwards limestone and Fredricksburg group of Texas, probably being limited to the middle Albian (Stanton, 1947, pp. 87–88, pl. 60, figs. 10–12). Though specimens equivalent in size from Texas and from Baja California have similar nodose spiral ornamentation, the largest Baja California specimens exhibit a smooth and concave profile. This phenomenon may possibly indicate a distinction of subspecific magnitude between specimens from the two localities but probably is merely the result of a more advanced stage of maturity reached in the larger Baja California specimens.

An additional difference in specimens from the two areas is in the nature of the

internal parietal folds. These folds are expanded distally in the Texas specimens but not in the sectioned Punta China specimens. A low proximal swelling on the posterior surface of these folds observed in several Punta China sections appears to be completely unrelated, never approaching the condition noted by Stanton (see Stanton, 1947, pl. 60, fig. 8). A comparison of many sections from both Texas and Baja California might reveal that this variation occurs within specimens from a single locality.

NERINEA (PLESIOPTYGMATIS) BÖSEI
Allison, n. sp.
Pl. 43, fig. 11; Text-fig. 3A

Shell moderately small, high-spired; spire profile convex posteriorly; sutures indistinct; volutions probably 10–15, very slightly concave to very slightly convex in profile; whorl diameter more than twice height; adult whorls with seven very low and smoothly rounded spiral ribs, evenly spaced except second which is closer to first than to third rib; first and seventh ribs closer to anterior slit-band margin and to anterior suture respectively than to adjacent spiral ribs; slit-band about equal in width to rib interspaces; pigmentation spots occupying very slight depressions along summits of spiral ribs, irregularly spaced, about 40–50 per whorl on each spiral rib; body whorl slightly flared anteriorly, at sharp angle with base; base of body whorl flat, with six low ribs commencing short distance inside periphery; internally with one slender columellar fold, one secondary columellar fold (not always developed), one parietal fold, and one labial fold; primary columellar and parietal folds long and slender, the former

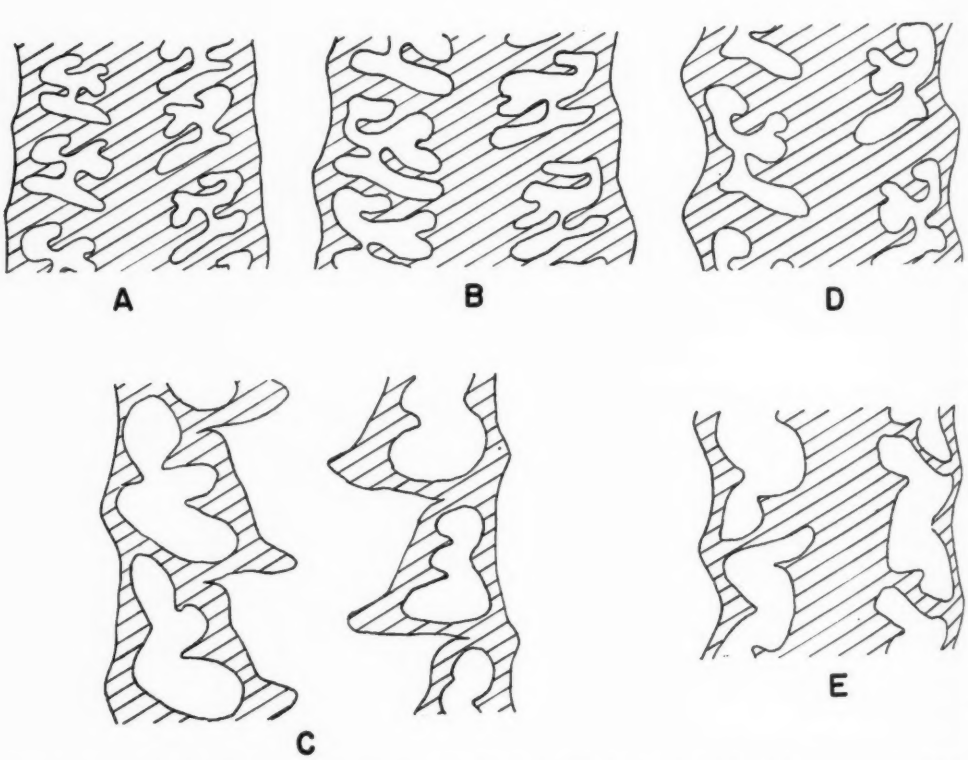

FIG. 3—Longitudinal sections of Nerineidae. A, *Nerinea* (*Plesioptygmatis*) *bösei* Allison, n. sp., ×4.5; B, *Nerinea* (*Plesioptygmatis*) *tomásensis* Allison, n. sp., ×1.6; C, *Diozoptyxis* cf. *D. pilgrimi* (Cox), ×1; D, *Cossmannea* (*Eunerinea*) *pauli* (Coquand), ×0.9; E, *Nerinea* (*Plesioptygmatis*) *tomásensis* Allison, n. sp., ×5.

with posterior swelling at or near distal end; labial fold slender, with approximately parallel sides.

Holotype.—No. 33621, loc. A-8321. Paratypes: nos. 33622 (Text-fig. 3A), 33623, loc. A-8313; nos. 33610, loc. A-8317; nos. 33626, 33627, 33617, 33618, loc. A-8321.

Dimensions.—Holotype: height (four last whorls) 23.5 mm., diameter 11.9 mm.

Occurrences.—Punta China, locs. A-8312 (C), A-8317 (F), and A-8321 (C).

Remarks.—*N.* (*P.*) *bösei* n. sp. differs from *N.* (*P.*) *tomásensis* n. sp., with which it frequently occurs, in its smaller size, lower and less straight-sided spire profile, and most important, in its almost straight-sided whorl profile as compared to the deeply concave whorl profile of *N.* (*P.*) *tomásensis* n. sp. Internally shells of the two species are almost identical, showing similar variation. The folds, particularly the parietal folds of *N.* (*P.*) *bösei* n. sp. are in general more slender.

NERINEA (PLESIOPTYGMATIS) TOMÁSENSIS Allison, n. sp.

Pl. 43, figs. 10, 12; Text-figs. 3B, 3E

Shell large, very high-spired; volutions exceedingly numerous, deeply concave in profile; whorl diameter about two and a half times corresponding whorl height; sutures elevated, bordered anteriorly and posteriorly by two irregular nodose cords; central area of whorl sharply concave on early whorls, more smoothly but still deeply concave on later whorls; width and nodosity of cords decreases anteriorly on spire; area between cords smooth except for coarse growth lines on latest whorls, sometimes with two irregular spiral ribs on early whorls; body whorl flared anteriorly, base smooth and at about right angle to side of whorl; aperture outline rhombohedral, with one columellar and one parietal fold visible; internally whorls show one columellar fold, one labial fold, and one parietal fold; secondary columeller fold and swelling on whorl floor often developed; secondary parietal flexure occasionally developed.

Holotype.—No. 33614, loc. A-8313. Paratypes: nos. 33766 (fig. 10), 33767 (Text-fig. 3B), 33768 (Text-fig. 3E), 33751–33753, 33755–33758, 33759, 33769–33772, loc. A-8313.

Dimensions.—Holotype: height (most of last four whorls) 80 mm., diameter 46 mm., apical angle less than 10°.

Occurrences.—Punta China, locs. A-8312 (F), A-8313 (A), A-8314 (C), A-8315 (F), A-8316 (R), A-8317 (F), A-8323 (C).

Remarks.—*N.* (*P.*) *tomásensis* n. sp. is one of the most spectacularly and abundantly represented fossils occurring at Punta China. In at least one instance the accumulation of individuals is so great that they form a biostromal limestone.

The species is characterized by its very high straight spire profile, low and deeply concave whorl profile, and by its lack of well marked spiral ornamentation other than the two cords bordering the sutures. One of the many closely related species, *Nerinea gemifera* Coquand var. *subgigantea* Blanckenhorn from the Cenomanian and Turonian of North Africa (see Delpey, 1939, pp. 194–195, pl. 7, fig. 10) has a much less concave whorl profile. *N.* (*P.*) *bösei* n. sp. which frequently occurs with *N.* (*P.*) *tomásensis* n. sp. has a smooth and well inflated spiral profile. Internally shells of the two species are often difficult to differentiate.

Genus APTYXIELLA Fischer

Aptyxiella FISCHER, 1885, Man. Conch., p. 689.

Type species: *Nerinea sexcostata* d'Orbigny.

Subgenus APTYXIELLA s. s.

APTYXIELLA (APTYXIELLA) cf. A. (A.) SUBULA (Roemer)

Pl. 43, figs. 3, 4

Hypotypes.—No. 33712 (fig. 3), loc. A-8317; no. 33713 (fig. 4), loc. A-8321.

Occurrences.—Punta China, locs. A-8317 (F), and A-8321 (F).

Remarks.—The Punta China specimens differ from *Aptyxiella* (*Aptyxiella*) *subula* (Roemer) as figured by Stanton (1947, pl. 62, figs, 3, 4) principally by their smaller size. The largest specimens collected at Punta China are only about half the size of the Texas specimens yet have practically lost all traces of spiral ornamentation while developing a semi-concave whorl profile. Specimens exhibiting spiral ornamentation similar to that of Stanton's specimens are even smaller. Internally the Baja California

specimens, as those from Texas, are without folds or plications.

Subgenus ENDIATRACHELUS Cossmann

Endiatrachelus COSSMANN, 1898, Mém. Soc. Géol. France, Pal., tome 8, no. 1, p. 134.

Type species: *Nerinea erato* d'Orbigny.

APTYXIELLA (ENDIATRACHELUS) PARALLELA (Anderson & Hanna)
Pl. 43, figs. 8, 9

[?]*Nerinella* sp. NAGAO, 1934, Jour. Faculty Sci., Hokkaido Imp. Univ., ser. 4, vol. 2, no. 3, pp. 251–252, pl. 38, figs. 8–10.
Turritella parallela ANDERSON & HANNA, 1935, Proc. Calif. Acad. Sci., ser. 4, vol. 23, p. 26, pl. 9, figs. 1–3.
Nerinea quadrilineata STANTON, 1947, U. S. Geol. Survey Prof. Paper 211, pp. 88–89, pl. 62, figs. 1–2.

Hypotypes.—No. 33714 (fig. 9), loc. A-8321; no. 33715 (fig. 8), loc. A-8331.

Occurrences.—Punta China, locs. A-8321 (F), A-8322 (F), and A-8331 (C).

Remarks.—This species would appear to have a widely extended geologic range on the basis of its reported occurrences. The Texas occurrences (referred to as *Nerinea quadrilineata*) in the Edwards limestone and Glen Rose limestone probably range between the top of the Aptian and the base of the upper Albian. A questionable occurrence in the Hiraiga sandstone of Honshu, Japan, is similar in age. Anderson and Hanna in their description of the species place it in the "Upper Senonian" Catarina formation of Baja California. Abundant specimens of this species at Punta China and further south at Punta San Isidro in Middle Cretaceous strata underlying equivalents of the Catarina formation would indicate an incorrect stratigraphic allocation of the holotype unless the Catarina specimens were derived from reworked older sediments.

A. (E.) parallela at its highest Punta China occurrence is represented by a form with a feebly developed anterior columellar fold as compared with that of the typical variety lower in the section. Exteriorly the modified form has but two strongly nodose spirial ribs (Pl. 43, fig. 9), the others being represented by feeble, non-noded ribs. Though this variety is larger than the typical, insufficient representatives are available to determine whether or not the differences are ontogenetic.

Genus COSSMANNEA Pčelincev

Cossmannea PČELINCEV, 1927, Mém. Com. Géol. Leningrad (N. S.), Livr. 172, p. 98.

Type species: *Nerinea desvoidyi* d'Orbigny.

Subgenus EUNERINEA Cox

Eunerinea COX, 1949, Proc. Malac. Soc. London, vol. 27, pt. 6, p. 250.

Type species: *Nerinea castor* d'Orbigny.

COSSMANNEA (EUNERINEA) PAULI (Coquand)
Text-fig. 3 D

Nerinea pauli COQUAND, 1862, Mém. Soc. Emul. Provence, tome 2, p. 177, pl. 4, fig. 3; —, DELPEY, 1939, Notes et Mém. Soc. d'Études Géol. Haut. Comm. Rep. Française en Syrie et au Liban, vol. 3 (1940), pp. 178–179, pl. 5, figs. 1–2, text fig. 2.
Nerinea cf. *N. gigantea* d'Orbigny. KNIPSCHEER, 1938, K. Akad. Wetensch. Amsterdam Proc., vol. 41, no. 6, p. 676, figs. 12, 13.

Hypotype.—No. 33718, loc. A-8311.

Occurrence.—Punta China, loc. A-8311 (R).

Remarks.—This species is reported from the Mediterranean area where it occurs in "Urgonian" and Aptian strata. The Provincial limestone[1] of Cuba contains a species to which Knipscheer (1938, p. 676) refers as "*Nerinea* cf. *N. gigantea* d'Orbigny" but which probably is conspecific with the Punta China species.

Genus DIOZOPTYXIS Cossmann

Diozoptyxis COSSMANN, 1896, Essais Paléonch. Comp., tome 2, p. 31.

Type species: *Nerinea monilifera* d'Orbigny.

DIOZOPTYXIS cf. D. PILGRIMI (Cox)
Text-fig. 3 C

Hypotype.—No. 33719, loc. A-8312.

Occurrence.—Punta China, loc. A-8312 (R).

Remarks.—The single broken specimen from Punta China closely resembles *Diozoptyxis pilgrimi* (Cox) from the Cenomanian or Turonian of Iran (Cox, 1936,

[1] The Provincial limestone is probably of Albian age according to MacGillavry (1939, p. 150).

Geol. Surv. India, vol. 22, Mem. 2, pp. 22–23, pl. 3, figs. 1a–b) both in exterior morphology and interior arrangement of wide umbilicus and plicated body chambers. The Punta China specimen, however, has a smaller apical angle though it has attained about the same diameter.

Superfamily STROMBACEA
Family APORRHAIDAE
Genus ANCHURA Conrad

Anchura CONRAD, 1860, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 4, p. 285, pl. 47, fig. 1.

Type species: *Anchura abrupta* Conrad.

Subgenus ANCHURA s. s.
ANCHURA (ANCHURA) ANDERSONI
Allison, n. sp.
Pl. 44, fig. 3

Shell moderately small, high-spired; volutions nine or ten; sutures impressed; whorl profile sharply angled anteriorly from center, low; diameter of whorl about twice height; anterior canal extended, outer lip of aperture with posterior digitation fused to penultimate whorl, extending to at least center of that whorl; a slender digitation, probably moderately long and straight, extending perpendicularly outward from center of outer lip, represents projection of main spiral carina; posterior portion of outer lip slightly turned back, thickened; inner lip with heavy callous; strong shoulder formed by main carina of body whorl, sharp, flanked anteriorly by a secondary carina; tertiary spiral ribs of body whorl distributed three posterior from main carina, two between main and secondary carinae, and six anterior from secondary carina; very fine spiral ribs over entire whorl surface; ornamentation of preceding whorls similar to that of body whorl or with about 15 strongly developed axial ribs giving whorl profile rounded rather than angular appearance.

Holotype.—No. 33745, loc. A-8331. Paratypes: nos. 33746–33750, 33774–33776, loc. A-8331.

Dimensions.—Holotype: height (almost complete) 21.8 mm., diameter about 17 mm., apical angle 35°.

Occurrence.—Punta China, loc. A-8331 (C).

Remarks.—*A.* (*A.*) *andersoni* n. sp. is closely related to "*Rostellaria*" *tricostata* d'Orbigny (1842–43, p. 287, pl. 207, fig. 8) from the Albian of Europe. The latter species differs from the Punta China species by its less well developed spiral ornamentation and apparent lack of axial ribs. Axial ribs, though variable, are consistently present on specimens of *A.* (*A.*) *andersoni* n. sp.

Subgenus PERISSOPTERA Tate

Perissoptera TATE, 1865, Geol. Nat. Hist. Repertory, vol. 1, p. 98.

Type species: *Rostellaria reussi* Tate.

ANCHURA (PERISSOPTERA) HANNAI
Allison, n. sp.
Pl. 44, fig. 2

Shell moderately small, high-spired; volutions about nine; whorl diameter over twice height, profile strongly convex with point of maximum convexity approximately at whorl center; later whorls ornamented by about fourteen heavy and smoothly rounded axial ribs; axial ribs concave posteriorly; superimposed spiral ornamentation of approximately fifteen narrow ribs; subdued axial ribs of body whorl represented by spiral keel at point corresponding to highest development of axial ribs on preceding whorls; body whorl keel extended outward and slightly posterior from outer lip as long slender digitation at angle of about 55° to axis; two additional but very short digitations extend perpendicularly and slightly anteriorly respectively from outer lip, fused together; anterior canal long, possibly curved; about twenty spiral ribs on anterior portion of body whorl, similar to those of spire; posterior portion of outer lip thickened, extending to penultimate whorl.

Holotype.—No. 33778, loc. A-8321. Paratypes: nos. 33779, 33780, loc. A-8321.

Dimensions.—Holotype: height (most of anterior canal missing) 21.9 mm., diameter slightly less than 10 mm., apical angle about 42°.

Occurrences.—Punta China, locs. A-8317 (?) (R), and A-8321 (F).

Remarks.—This species is distinguished from such related species as *A.* (*P*). *marginata* (Sowerby) from the Gault of Folkestone (see Cossmann, 1904, pl. 6, fig. 3) by the character of the outer lip digitations. In addition Sowerby's species lacks the semi-

angular whorl profile of *A.* (*P.*) *hannai* and exhibits an additional short fused digitation on its outer lip.

Superfamily NATICACEA
Family NATICIDAE
Genus NATICA Scopoli

Natica SCOPOLI, 1777, Intr. Hist. Nat., p. 392.

Type species (by subsequent designation, Harris, 1897): *Nerita vitellus* Linnaeus.

NATICA IMPORTUNA Nagao
Pl. 44, fig. 7

Natica importuna NAGAO, 1934, Jour. Faculty Sci., Hokkaido Imp. Univ., ser. 4, vol. 2, no. 3, pp. 244–245, pl. 35, figs. 8, 9, 15.

Hypotype.—No. 33736, loc. A-8321.

Occurrences.—Punta China, locs. A-8317 (F) and A-8321 (A).

Remarks.—Nagao's specimens from the Hiraiga sandstone of the Miyako District, Honshu, Japan (probably upper Aptian or Albian) are in general larger than those collected at Punta China. Several of the Punta China specimens show a pigmentation pattern of two wide, dark spiral bands on the body whorl; only the posterior appearing on the penultimate whorl. The posterior band of the body whorl is limited anteriorly at about the whorl midpoint and extends posteriorly to about halfway between midpoint and suture. The anterior band is narrower and is separated from the posterior band by a space about equal in width to the space between posterior band and suture.

NATICA JAPONICA (Nagao)
Pl. 44, fig. 9

Vanikora japonica NAGAO, 1934, Jour. Faculty Sci., Hokkaido Imp. Univ., ser. 4, vol. 2, no. 3, pp. 245–247, pl. 38, figs. 3–6.

Hypotype.—No. 33737, loc. A-8331.

Occurrences.—Punta China, loc. A-8331 (A).

Remarks.—This species occurs in the Hiraiga sandstone (upper Aptian or Albian) of the Miyako District, Honshu, Japan. The Punta China specimens sometimes exhibit a few very fine, closely spaced spiral furrows on the posterior part of the body whorl. The spiral pigmentation pattern consists of about fifteen equally spaced dark lines on the body whorl, each about equal in width to a quarter of the width of adjacent interspaces.

Subfamily EUSPIRINAE
Genus TYLOSTOMA Sharp

Tylostoma SHARP, 1849, Quart. Jour. Geol. Soc. London, vol. 5, p. 378.

Type species: *Varigera ricordeana* d'Orbigny.

Subgenus TYLOSTOMA s. s.

TYLOSTOMA (TYLOSTOMA) MUTABILIS Gabb
Pl 44. fig. 8

Tylostoma mutabilis GABB, 1869, Geol. Survey California, Paleontology, vol. 2, pp. 261–262, pl. 35, figs. 6a–c; ——, KING, 1939, Geol. Soc. America, Bull., vol. 50, p. 1670.

Hypotype.—No. 33741, loc. A-8317 (C).

Remarks.—This species occurs in the "Potrero" formation near Arivechi, Sonora, México, and in the Fredricksburg group of Central Texas. Its probable age is therefore middle Albian. *Tylostoma miyakoensis* Nagao (1934, pp. 247–248, pl. 34, figs. 1–3, 6, 7, pl. 39, fig. 3) from the *Orbitolina* sandstone, Hiraiga sandstone, and Moshi sandstone of Honshu, Japan, is very similar to the American species.

TYLOSTOMA (TYLOSTOMA) cf. T. (T.) MATERINUM White
Pl. 44, fig. 16

Hypotype.—No. 33732, loc. A-8321.

Occurrence.—Punta China, loc. A-8321 (F).

Remarks.—The Punta China specimen is slightly distorted but clearly exhibits more impressed sutures and a higher spire than White's species from the middle Albian of Brazil (White, 1887, Arch. Mus. Nat. Rio de Janeiro, vol. 17, p. 189, pl. 17, fig. 1; Maury, 1936, Brazil, Serv. Geol. Miner., Mon., vol. 11, pp. 196–197, pl. 15, fig. 2, pl. 16, fig. 1.

Order NEOGASTROPODA
Superfamily BUCCINIACEA
Family FASCIOLARIIDAE
Genus EUTHRIOFUSUS Cossmann

Euthriofusus COSSMANN, 1901, Essais Paléonch., tome 4, pp. 27–29.

Type species.—*Fusus burdigalensis* Basterot.

EUTHRIOFUSUS WENZI Allison, n. sp.
Pl. 44, figs. 10–12

Shell small, moderately low-spired; volutions about six, strongly shouldered; whorl

diameter less than twice corresponding height; aperture wide, extending gradually into straight anterior canal; spire whorls straight-sided; body whorl anteriorly angulated approximately at mid-point, sloping at about 35° angle to shell axis posteriorly; whorl ornamentation of about fifteen axial ribs and eight primary spiral ribs alternating with finer raised lines; anterior part of body whorl with gradually subdued axial ribs and about eight primary spiral ribs; outer lip of aperture thin, inner lip narrowly callused, smooth.

Holotype.—No. 33782, loc. A-8331. Paratypes: nos. 33783 (fig. 11), 33784 (fig. 12), 33785–33787, loc. A-8331.

Dimensions.—Holotype: height (incomplete) 14.0 mm., diameter about 10 mm., apical angle about 60°.

Occurrence.—Punta China, loc. A-8331 (C).

Remarks.—*Euthriofusus wenzi* n. sp. resembles *E. mesozoicus* (Wade) from the Ripley formation of Tennessee (Proc. Acad. Nat. Sci. Philadelphia, vol. 69, p. 284, pl. 17, figs. 11, 12) in general shape and nature of ornamentation. The species described by Wade has less pronounced axial ribs and probably a longer anterior canal than the Punta China species, though the anterior portion is incomplete on all known specimens of the latter.

Subclass OPISTHOBRANCHIA
Order PLEUROCOELA (TECTOBRANCHIA)
Superfamily ACTAEONACEA
Family ACTAEONIDAE
Subfamily NUCLEOPSINAE
Genus LIOCARENUS Harris & Burrows

Liocarenus HARRIS & BURROWS, 1891, Eocene and Oligocene beds of the Paris Basin, pp. 98, 113.

Type species.—*Auricula conovuliformis* Deshayes.

Subgenus LIOCARENUS s. s.
LIOCARENUS (LIOCARENUS) FORMOSUM (Cragin)
Pl. 44, fig. 13

Cylindrites formosus CRAGIN, 1893, Texas Geol. Survey Ann. Rept., vol. 4, p. 223, pl. 24, fig. 4; ——, ADKINS, 1928, Texas Univ. Bull. 2838, p. 195.

[?] *Acera eliai* SHALEM, 1928, Soc. Geol. Italiana, Boll. vol. 47, fasc. 1, pp. 99–100, pl. 5, figs. 38a–h; ——, Blanckenhorn, 1934, Palaeontographica, Band 81, abt. A, p. 275, pl. 14, figs. 200 a, b.

Tylostoma ? formosum (Cragin). STANTON, 1947, U. S. Geol. Survey Prof. Paper 211, pp. 68–69, pl. 52, figs. 6, 8.

Hypotype.—No. 33739, loc. A-8321.

Occurrence.—Punta China, loc. A-8321 (R).

Remarks.—Assignment of this species to the genus *Liocarenus* was made after an examination of specimens of the type species, *L. conovuliformis*, from the Paris Basin Eocene. The Punta China specimen lacks the very fine spiral sculpturing characteristic of that group but this could be due to inadequate preservation of the shell surface.

The range of variation among specimens of the type species from a single locality is probably sufficiently great to justify placing in synonomy the American (middle Albian ? of Texas) and the Near Eastern (lower Cenomanian of Jerusalem) species. This variation was noted also by Shalem in his original description of "*Acera eliai.*"

Family ORTHOSTOMIDAE
Genus ACTAEONELLA d'Orbigny

Actaeonella D'ORBIGNY, 1842, Paleontologie Française, Terrain Crétacé, vol. 2, p. 107.

Type species.—*Actaeon laevis* Sowerby.

ACTAEONELLA PARVUS (Stanton)
Pl. 44, fig. 5

Trochactaeon parvus STANTON, 1947, U. S. Geol. Survey Prof. Paper 211, p. 112, pl. 63, figs. 1–2.

Hyptotype.—No. 33740, loc. A-8321.

Occurrence.—Punta China, loc. A-8321 (F).

Remarks.—This species occurs in the Edwards limestone (middle Albian) of Texas. The Punta China representatives can be distinguished from juvenile specimens of *Actaeonella fusiformis* by the more inflated body whorl and much higher spire of the former.

ACTAEONELLA FUSIFORMIS Coquand
Pl. 44, figs. 1, 4

Actaeonella fusiformis COQUAND, 1865, Mém. Soc. Emul. Provence, vol. 3, p. 69, pl. 3, fig. 9; ——, DELPEY, 1939, Notes et Mém. Soc. d'Études Géol. Haut. Comm. Rép. Française en Syrie et au Liban, vol. 3 (1940), pp. 70–71, text figs. 44, 45.

Trochactaeon (*Actaeonella*) *fusiformis* STOLICZKA, 1868, Mem. Geol. Survey India, Palaeont. Indica, ser. 5, vol. 2, pt. 13, p. 418.

Hypotypes.—Nos. 33707 (fig. 1), 33708 (fig. 4) loc. A-8331.

Occurrences.—Punta China, locs. A-8314 (?) (R) and A-8331 (A).

Remarks.—This species occurs in the Aptian of the Mediterranean region. Adult specimens (slightly larger than the holotype which is 21 mm. long and 8 mm. in diameter) from Punta China (Pl. 44, fig. 1) agree very closely with the illustrations and description provided by Delpey (1939, pp. 70–71, text figs. 44, 45). Juvenile specimens from Punta China have similarly parallel sides of ultimate whorls (Pl. 44, fig. 4) but have a slightly elevated instead of sunken spire. Several very small specimens have body whorls which taper anteriorly from the shoulder but these appear to represent merely earlier ontogenetic stages of the same species.

A single, very large and heavy-shelled specimen of a sunken-spired *Actaeonella*-like gastropod was collected from locality A-8314, above the stratigraphic occurrence of *A. fusiformis* s. s. The anterior portion of this specimen is missing so its generic and specific assignments are questionable. It is about twice the size of adult specimens of *A. fusiformis*.

Family RINGICULIDAE
Genus OLIGOPTYCHA Meek

Oligoptycha MEEK, 1876, U. S. Geol. Survey Territories, Ann. Rept., vol. 9, pp. 283–284.

Type species.—*Actaeon concinnus* Hall & Meek.

OLIGOPTYCHA? POPENOEI Allison, n. sp.
Pl. 44, figs. 14, 15

Shell small, subglobose, moderately heavy; spire depressed; sutures distinct; volutions about three; aperture sublunate, narrow posteriorly; outer lip thickened, smooth inside and out, anteriorly entire except for slight depression representing siphonal canal; columella with two plications, the strongest of the pair close to anterior margin of aperture and at approximately a right angle to shell axis, the weakest about one-third of whorl height from anterior margin (not visible in figures); whorl ornamentation of about twenty-five narrow, equally spaced punctuate furrows separated by broad, flat-topped ribs.

Holotype.—No. 33710, loc. A-8331.

Dimensions.—Holotype: height 4.8 mm., diameter 4.3 mm.

Occurrence.—Punta China, loc. A-8331 (R).

Remarks.—This species resembles *"Oligoptycha" obliqua* (Gabb) from the Chico formation of California (see Stewart, 1926, p. 436, p. 24, fig. 14) which is probably incorrectly referred to this genus according to Stephenson (1941, p. 390). Gabb's species is lower and exhibits a slightly elevated spire, wider spiral furrows, and reversed relative development of the two columellar plications. A possibility that the Punta China species is also represented in the Cretaceous of California is suggested by the occurrence of a similar, though very poorly preserved, gastropod in the University of California collections which is probably from locality 2851 (Shasta County, California). *Lytoceras gainesi* and *Beudanticeras breweri* also occur at locality 2851.

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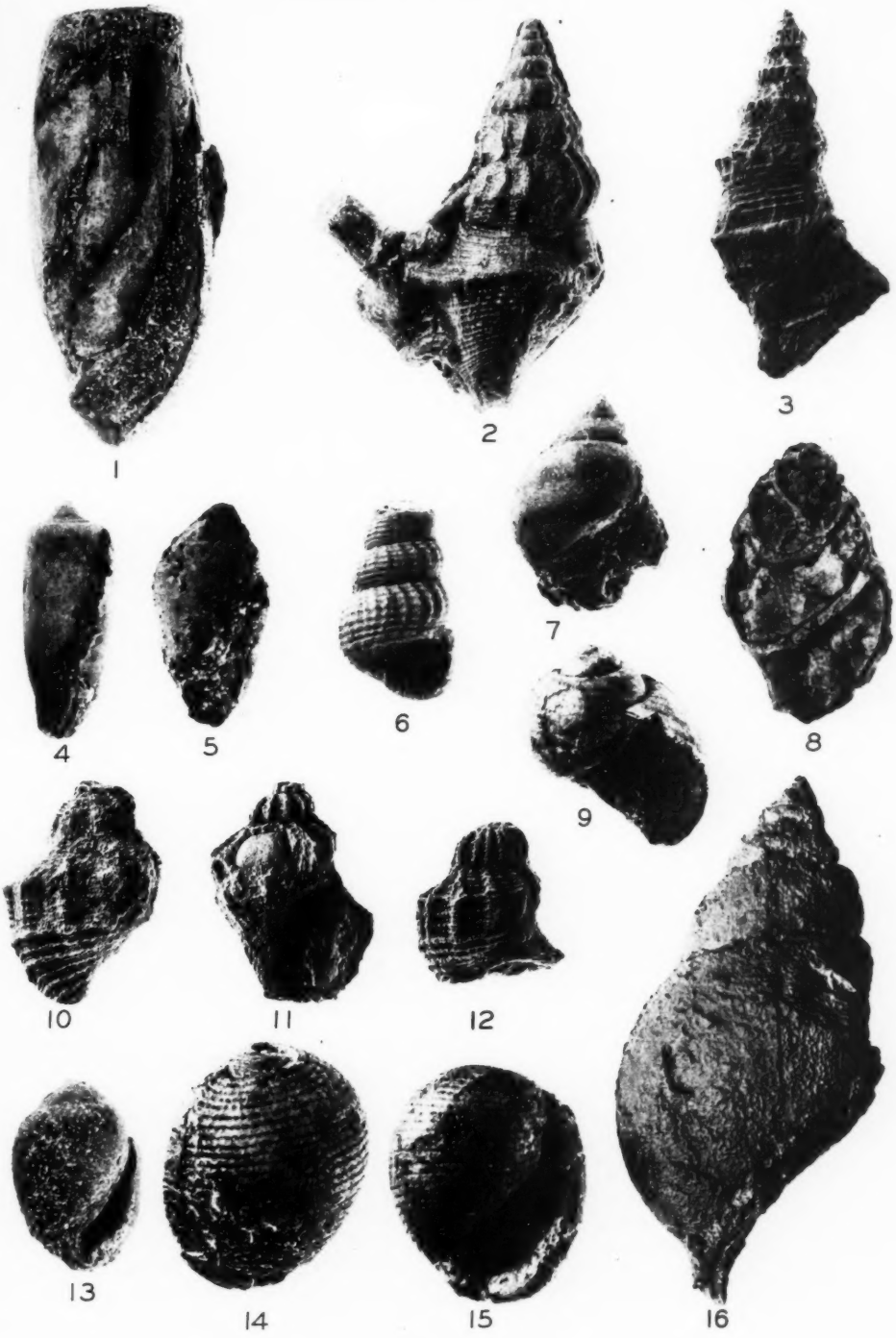
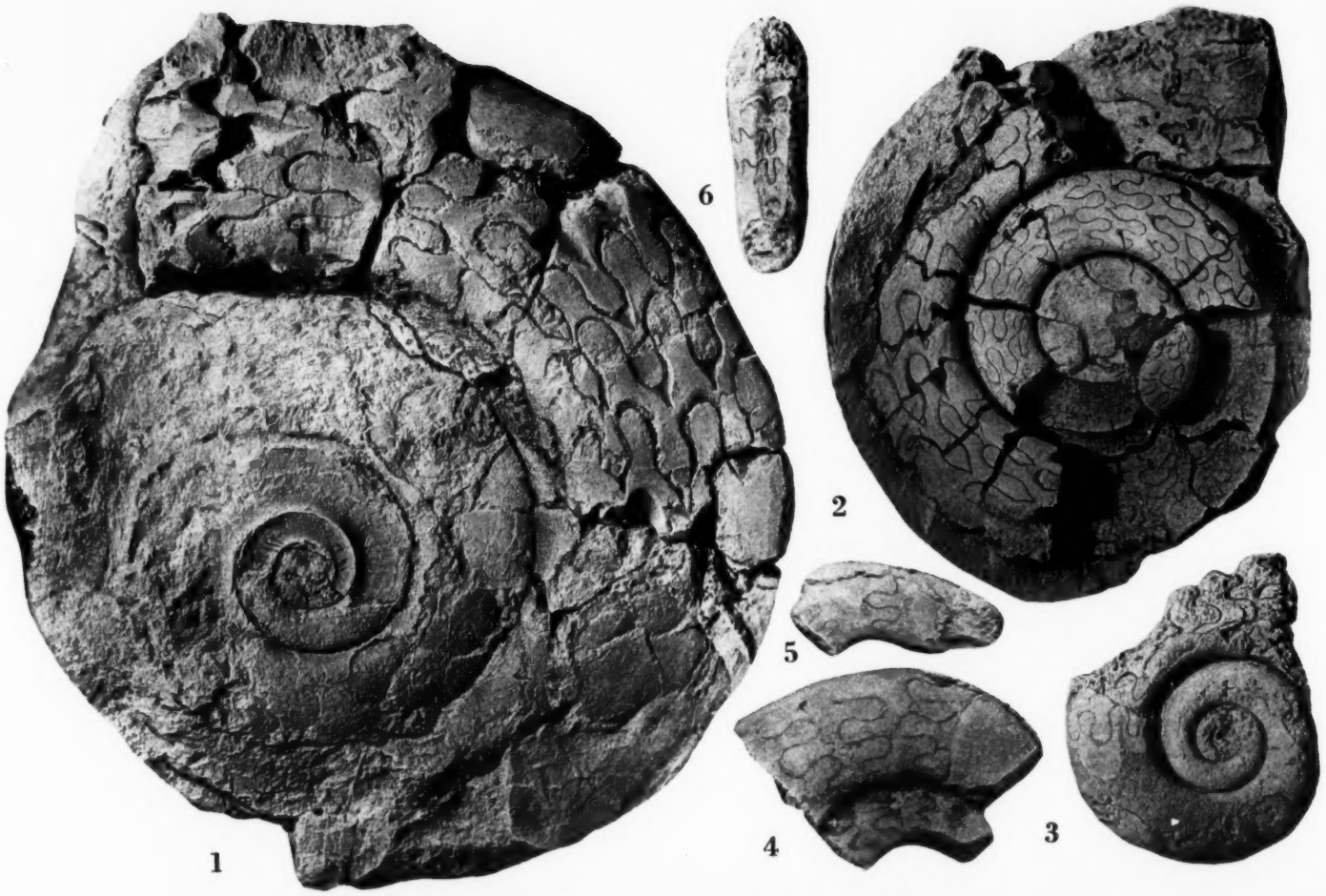
EXPLANATION OF PLATE 44

FIGS. *1*—*Actaeonella fusiformis* Coquand. Hypotype no. 33707, ×2.1. Loc. A-8331. (p. 429)
2—*Anchura* (*Perissoptera*) *hannai* Allison, n. sp. Holotype no. 33778, ×2.5. Loc. A-8321. (p. 427)
3—*Anchura* (*Anchura*) *andersoni* Allison, n. sp. Holotype no. 33745, ×2.3. Loc. A-8331. (p. 427)
4—*Actaeonella fusiformis* Coquand. Hypotype no. 33708, ×4.1. Loc. A-8331. (p. 429)
5—*Actaeonella parvus* (Stanton). Hypotype no. 33740, ×6.1. Loc. A-8321. (p. 429)
6—*Opalia* (*Crassiscala*) *riachuelanum* (Maury). Hypotype no. 33576, ×3.4. Loc. A-8331. (p. 422)
7—*Natica importuna* Nagao. Hypotype no. 33736, ×3.7. Loc. A-8321. (p. 428)
8—*Tylostoma* (*Tylostoma*) *mutabilis* Gabb. Hypotype no. 33741, ×1.1. Loc. A-8317. (p. 428)
9—*Natica japonica* (Nagao). Hypotype no. 33737, ×2.1. Loc. A-8331. (p. 428)
10–12—*Euthriofusus wenzi* Allison, n. sp. *10*, Holotype no. 33782, ×2.1; *11*, Paratype no. 33783, ×2.3; *12*, Paratype no. 33784, ×2.2. All Loc. A-8331. (p. 428)
13—*Liocarenus* (*Liocarenus*) *formosum* (Cragin). Hypotype no. 33739, ×3.0. Loc. A-8321. (p. 429)
14, 15—*Oligoptycha? popenoei* Allison, n. sp. Holotype no. 33710, ×5.3. Loc. A-8331. (p. 430)
16—*Tylostoma* (*Tylostoma*) cf. *T.* (*T.*) *materinum* White. Hypotype no. 33732, ×0.6. Loc. A-8321. (p. 428)



Allison, Middle Cretaceous Gastropoda, Baja California



Collinson, Mississippian goniatites, Illinois

JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 433–438, PL. 45, 2 TEXT-FIGS., MAY 1955

MISSISSIPPIAN PROLECANITID GONIATITES FROM ILLINOIS AND ADJACENT STATES[1]

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ABSTRACT—The Mississippian prolecanitid goniatite genera *Merocanites* and *Prolecanites* are stratigraphically useful in Europe but seem to be rare in America. *M. drostei*, n. sp., from the Brodhead formation of Kentucky is described and illustrated, as are three specimens of *P. monroensis* (Worthen) from the Ste. Genevieve limestone of Illinois. *P. americanus* Miller and Garner from Greencastle, Indiana, is very close to *P. monroensis* and probably is Ste. Genevieve (upper Meramec) in age.

INTRODUCTION

For many years European stratigraphers have recognized the significance of the Lower Carboniferous cephalopod genera *Protocanites*, *Merocanites*, and *Prolecanites*. These forms are members of a phylogenetic series which has been carefully worked out in Europe, mainly by Bisat, Schindewolf, and Schmidt; and stratigraphers have used the series with considerable success for both interbasinal and intercontinental correlation. The Prolecanitidae, the family to which these genera belong, consists of evolute, discoidal goniatites whose sutures form rounded saddles and linguliform lobes. They evolved by increasing the number of lateral lobes in their external sutures. In general, the greater the number of lateral lobes, the more advanced the genus.

The polylogenetic series began in the Tournaisian with *Protocanites*, which possesses an external suture with a simple V-shaped ventral lobe and two pairs of lateral lobes, (plus a pair of lobes on the umbilical seams). In the lower and early middle Viséan the series progressed through *Merocanites*, which has a lanceolate ventral lobe and three lateral lobes, and in the middle and upper Viséan appeared *Prolecanites*, with four lateral lobes.

Of the three genera only *Protocanites* is of widespread occurrence in North America, and it is widely recognized as an index of early Lower Carboniferous age not only in North America and Europe, but in Asia, Africa, and Australia as well.

Merocanites is well known only in Europe, where it ranges from lowermost Viséan (Vaughn's C_2 and Schmidt's II γ zones) up into the lower middle Viséan (Bisat's *Beyrichoceras* zone and Schmidt's zone III α). Thus the "zone of *Merocanites*" occurs between the *Protocanites* zone characteristic of the European Touranisian, as well as the North American Kinderhook, and Schmidt's zone of *Goniatites* (Bisat's P_1 zone and Schmidt's zone III β).

Schmidt (1925, p. 539) first reported the

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EXPLANATION OF PLATE 45

FIGS. *1*, *2*—*Merocanites drostei* Collinson, n. sp. *1*, the holotype, from the Brodhead formation of Madison County, Kentucky; ×1. *2*, a paratype from the same locality and horizon as the holotype; ×1. (p. 434)

3–6—*Prolecanites monroensis* (Worthen). *3*, the holotype from the Ste. Genevieve limestone of Monroe County, Illinois; ×1. *4*, immature portion of an incomplete topotype (showing external sutures) found in the same piece of limestone as the holotype; ×3. *5*, *6*, lateral and dorsal views of a fragment of a topotype (showing both external and internal sutures) found in the same piece of limestone as the holotype; ×1 and 1.2, respectively. (p. 436)

American occurrence of *Merocanites* when he recognized as members of the genus *M. marshallensis* (Winchell) and *M. houghtoni* (Winchell) from the Marshall group of Michigan. Since that time no other members of *Mercanites* have been reported from the Americas, although a search through the literature has revealed that the form described in 1894 by S. A. Miller as "*Goniatites greenii*" from the "Knobstone Group," near New Albany, Indiana, most certainly belongs in *Merocanites*.

Early last year I acquired three representatives of *Merocanites* from the Brodhead formation of Madison County, Kentucky. Because these specimens represent an undescribed form, I am naming the new species in honor of Mr. John Droste, of the University of Illinois, who collected the fossils.

Prolecanites also is well known only in Europe, where it occurs in a zone which ranges from middle Viséan (Vaughn's D_1 zone and Schmidt's zone III α) up to about the base of the Namurian (Bisat's E_1 zone and Schmidt's zone IV_1). The "zone of *Prolecanites*" nearly coincides with the occurrence of *Goniatites* s. s. and overlaps the occurrence of both *Beyrichoceras* and *Merocanites*.

In 1953 Miller and Garner reported the first-known American species of *Prolecanites* s. s. and coined for it the name *P. americanus*. However, the collections of the University of Illinois contain another species which should be referred to the genus—Worthen's holotype of *Goniatites monroensis* from the Ste. Genevieve oolitic limestone of Monroe County, Illinois. Because Worthen's description and illustrations are in error and because of the stratigraphic significance attached to the genus, *Prolecanites*, I am reillustrating and describing the holotype as well as two incomplete specimens of the same species which were in the piece of limestone which yielded the holotype.

I am indebted to Professors A. K. Miller and W. M. Furnish of the State University of Iowa, and to Mr. Brian Glenister of the University of Western Australia, who is, at present, at the State University of Iowa on an international scholarship. All critically read the manuscript and offered suggestions for its improvement.

MEROCANITES DROSTEI Collinson, n. sp.
Pl. 45, figs. 1, 2

The specimens are three well-preserved but fragmentary internal molds, all of which are preserved in iron carbonate concretions. The most fragmentary of the three individuals consists of portions of two whorls, representing about one-fourth volution of an immature whorl and a single camera of a mature whorl. When complete, this individual had a maximum diameter of at least 90 mm. The other two specimens represent internal molds of individuals which were at least 75 and 120 mm. in diameter. The smaller of these (Pl. 45, fig. 2) is completely septate and consists of three-fourths of a well-preserved immature whorl and one-fourth of an early mature whorl in contact with it. An external mold of the missing portions of the specimen is preserved. The largest of the three specimens, which is here designated the holotype, consists of at least six volutions, of which only the adoral one-fourth of the outer volution is septate. All but the septate portion is crushed, and much of the specimen retains the shell or a replacement of it. The innermost three or four volutions are preserved as an external mold. Growth lines are exhibited by all three specimens. They can be seen to form broadly rounded lateral salients and to curve apicad on the umbilical walls to form sinuses (Pl. 45, fig. 1).

The holotype is discoidal, compressed, and evolute. At maturity the whorls are subrectangular in cross section (Text-fig. 1C), being more than twice as high as wide. The greatest width is attained near the mid-height, the venter is broadly rounded, the flanks are nearly flat, and the dorsum is slightly impressed. The umbilicus is large, and the umbilical walls are rounded. It is difficult to determine the rate of expansion of the holotype because of its partially crushed state. However, by using measurements from both the holotype and the figured paratype, I have compiled Table 1.

As shown by Text-fig. 1A, each mature suture forms a small V-shaped ventral lobe and on each side of it is a rounded asymmetrically U-shaped first lateral saddle, a deep lanceolate first lateral lobe, a second lateral saddle more or less U-shaped (though higher, more constricted, and more narrowly

TABLE 1.—DIMENSIONS TAKEN FROM THE FIGURED TYPES OF *Merocanites drostei*, N. SP.

	Holotype	Figured Paratypes		
	mm.	mm.	mm.	mm.
External diameter	115	43	37	29
Whorl height	30	12	11½	10
Whorl width	10	6	5½	5
Depth of dorsal impression	2½			
Umbilical diameter	65	20	15	14

rounded than the first), a second lateral lobe similar to the first but larger and deeper, an asymmetrical U-shaped third lateral saddle, a third lateral lobe smaller than the first, an asymmetrical narrowly rounded umbilical saddle well outside the umbilical shoulder, and an asymmetrical angular umbilical lobe centered just inside the umbilical shoulder. The dorsal lobe is deep and narrow, and on each side of it is a narrow U-shaped dorsal saddle. The early mature sutures are essentially the same as the fully mature sutures, differing only in that the third lateral lobe is relatively small and the dorsal saddles are very narrow.

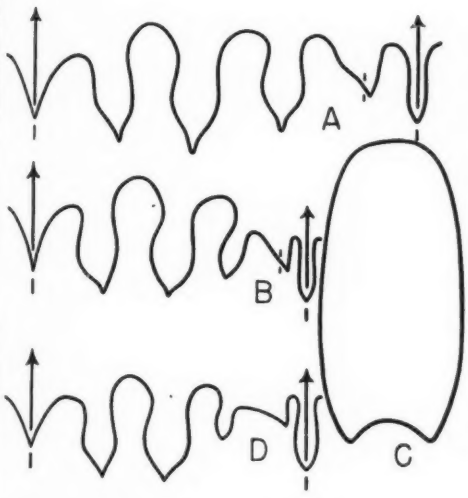

FIG. 1—Diagrammatic representations of sutures and cross sections of *Merocanites*. A, mature suture based on the holotype of *M. drostei* at a whorl height of 20 mm.; ×1.5. B, early mature suture based on the figured paratype of *M. drostei* at a whorl height of 12 mm.; ×2.5. C, cross section of a whorl of the holotype of *M. drostei*, taken at the same place as A; ×1.3. D, suture based on a paratype of *M. subapplantus* Smyth from the Rush slates, Co. Dublin, Ireland, taken at a whorl height of 16 mm. (after Smyth); ×1.67.

Remarks.—This species is very closely related to the type species of *Merocanites*, *M. compressus* Sowerby, from the lower Viséan of Yorkshire and Lancashire in England, Westphalia in German, and County Cork in Ireland. Both forms are large and appear to have similar cross sections, although the whorls of *M. drostei* are more impressed dorsally than those of the type species and the latter is somewhat flatter around the periphery. The sutures of the two species are very similar, but the ventral lobes of *M. drostei* are considerably deeper and its umbilical lobes more acute than those of *M. compressus*.

Smyth (1951) considered his species, *M. subapplanatus* from the Rush slates of County Dublin, Ireland, to be very close to *M. compressus* (Sowerby), and it appears to be even closer to *M. drostei*. Sutures of the two species taken from whorls of equal height are quite similar. In the mature sutures of the Kentucky species, however, the third lateral lobes are somewhat larger than in the most mature sutures of the Irish form. When one considers this together with the fact that the largest specimen of *M. subapplanatus* is only 95 mm. in maximum diameter, compared to 115 mm. for the holotype of *M. drostei*, it seems that the latter might be a late mature representative of the former species. Cross sections of the whorls of the Irish species, however, are considerably wider than those of *M. drostei* and thus serve to distinguish the species.

Occurrence.—The specimens described are from the Conway Cut siltstone member of the Brodhead formation of the Osage group. They were found lying on the surface near the base of a 76-foot outcrop on the north side of Kentucky Highway 21, about 3.5 miles east-southeast of Berea, Madison County, Kentucky. Stockdale (1939, p. 175) described the outcrop which yielded the types. The siltstone yields many large iron carbonate concretions like the ones in which the specimens were found.

Repository.—Illinois State Geological Survey.

PROLECANITES MONROENSIS (Worthen)
Pl. 45, figs. 3–6

Goniatites monroensis WORTHEN, 1890, Illinois Geol. Survey, vol. 8, p. 150, pl. 16, fig. 5.

In the original description of this form, Worthen (1890, p. 150) stated that the "species is represented by a single specimen only." On examining the small piece of very buff oolitic limestone which contains the holotype, I discovered also embedded in it two well-preserved fragments of the same species. These two topotypes represent less than one-fourth of one early-mature whorl and slightly less than one-fourth volution of two juvenile whorls respectively (Pl. 45, figs. 3–6). Further study revealed that the original description and illustration of the holotype are grossly in error and that the three type specimens are referable to the genus *Prolecanites*. All three individuals are internal molds which are completely septate. They are illustrated on the accompanying plate.

The holotype is discoidal in shape and is about 45 mm. at greatest diameter. It consists of three and one-fourth volutions, all of which are septate. The conch is expanded rapidly orad and is higher than wide. It is subelliptical in cross section and is slightly impressed dorsally (Text-fig. 2D). The dimensions of the holotype are given in Table 2.

TABLE 2.—DIMENSIONS OF THE HOLOTYPE OF *Prolecanites monroensis* (WORTHEN)

	Millimeters		
External diameter	45	35	25
Whorl height	15	12	9
Whorl width	12	10	7.5
Diameter of umbilicus	19.5	14	10.5

The umbilicus of the holotype is open and wide. The umbilical shoulders are rounded and indefinite. Although much of the test, or a replacement of it, is preserved, no surface markings are discernible.

As indicated by Text-fig. 2A, each mature suture consists of twelve lobes and an equal number of saddles. The ventral lobe is large,

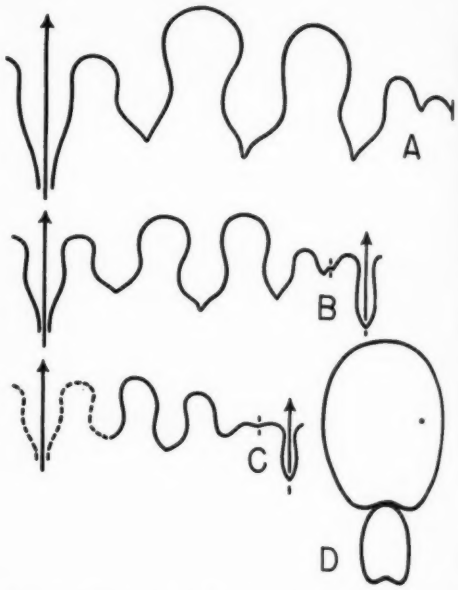

FIG. 2—Diagrammatic representations of *Prolecanites monroensis* (Worthen). A, mature suture based on the holotype at a whorl height of 12.5 mm.; ×3.5. B, early mature suture based on the topotype illustrated by Pl. 45, figs. 5, 6, at a whorl height of 9 mm.; ×3.0. C, immature suture based on the topotype illustrated by Pl. 45, fig. 4, at a whorl height of 2 mm.; approximately ×9. D, cross section of two whorls of the topotype illustrated by Pl. 45, fig. 4; ×3.5.

lanceolate, and attenuate. The first lateral saddle is U-shaped with straight sides. It is smaller than the lanceolate first lateral lobe, which is also relatively small. The second lateral saddle is large and asymmetrically U-shaped. The second lateral lobe, which is also large and deep, is lanceolate and is constricted laterally. It adjoins the third lateral saddle which is U-shaped and is intermediate in size between the first and second saddles. The third lateral lobe is very similar in shape to the first, but is slightly smaller. The fourth lateral saddle is U-shaped, asymmetrical, relatively deep, and small. The fourth lateral lobe is small and V-shaped though the sides are slightly convex. The broad, shallow, umbilical saddle centers outside the umbilical seam and extends across the seam to an internal lobe which cannot be seen in the holotype. In the topotypes, which represent juvenile portions of conchs, the internal lobes are simi-

lar to the external fourth lateral lobes of the holotype but are considerably smaller. The dorsal lobe is spatulate and is nearly as long as the ventral lobe. On each side of it there is a small U-shaped dorsal saddle. Fortunately, the early ontogenetic development of the sutures was ascertainable from the two small individuals. The early development of the sutures shows the fourth external lateral lobe and the internal lateral lobe to be adventitious. Furthermore, the early sutures seem to indicate that the ventral and lateral lobes evolved independently and that lateral lobes are added to the suture near the umbilicus and migrate ventrally until they reach full development and become stable in position.

Remarks.—The type species of *Prolecanites*, *P. mojsisovicsi* Miller from the Viséan of west-central Germany, appears to be close to *P. monroensis*. All elements of the sutures are closely similar with the exception of the fourth lateral lobes, which in the type species are deeper and closer to the umbilical seam than in the Illinois species. Unfortunately, the type species is not very well known and accurate detailed comparisons are not possible.

P. monroensis is remarkably close to *P. americanus* Miller and Garner. As can be seen by the following measurements taken from the illustrations (Miller and Garner, 1953, pl. 86, fig. 5, 6) of the holotype of the latter, the height, width, rate of expansion, and size of umbilicus of the conchs of the two species are similar.

TABLE 3.—DIMENSIONS OF THE HOLOTYPE OF *Prolecanites americanus* MILLER AND GARNER

	Millimeters	
External diameter	34	35
Whorl height	16	—
Whorl width	12½	9½
Diameter of umbilicus	19½	13½

The sutures likewise are very much alike although the ventral lobe of the Indiana species is shorter and narrower than that of *P. monroensis*, and the fourth lateral lobe is more acutely V-shaped.

A fact of stratigraphic importance is that both *P. americanus* and *P. monroensis* apparently came from rocks of the same age. Although the authors of *P. americanus* state that it came from the "Salem limestone at or near Greencastle, Putnam County, Indiana," I have reason to believe that it came from the Ste. Genevieve limestone. This assumption is based upon the fact that an outcrop of Ste. Genevieve (not Salem) completely surrounds the city of Greencastle, and that there are several quarries in the oolitic Ste. Genevieve near and in the city (D. H. Swann, 1954, personal communication). Further supporting evidence for a Ste. Genevieve age for *P. americanus* is given by Worthen and Shaw (1873, p. 275), who wrote of the locality from which the type of *P. monroensis* came:

> About ten feet in thickness of the limestone may be seen here, the lower three feet of which is a very hard shell breccia, largely composed of chambered shells belonging to the genera *Nautilus*, *Goniatites* and *Orthoceras*, and seems to be the exact equivalent of a similar bed occurring at Greencastle, Indiana, where the rock, though similar in character, is not so hard, and its characteristic fossils may be obtained much more easily, and in a better state of preservation. . . . The beds above this brecciated limestone, contain *Lithostrotion proliferum*, *Zaphrentis spinulosa*, etc., and are immediately overlain by the Chester sandstone.

It is also noteworthy that Worthen and Meek (1873, pp. 544–45) list both "*Nautilus* (*Temocheilus*) *Coxanus*, M. and W." and "*Nautilus* (*Solenocheilus*) *collectus*, M. and W." as occurring in the "St. Louis division of the Lower Carboniferous" at both Greencastle and Waterloo. In 1890 Worthen (p. 151) further listed *Solenocheilus indianense* Worthen and *Orthoceras* sp. as occurring in the cephalopod fauna from Greencastle; thus, of the cephalopods known from these two localities, it appears that only *Solenocheilus indianense* is not common to both localities.

Of the numerous European species of *Prolecanites*, *P. monroensis* is perhaps closest to *P. discoides* Foord and Crick from the Carboniferous limestone of England, probably Yorkshire. However, the conch of the former expands more rapidly and the flanks of its whorls are slightly though distinctly more convex than those of the latter. The sutures are similar, although the umbilical lobe of *P. discoides* is shallow and obtuse. The whorls of the conch are not indented dorsally.

If one allows for slight differences of interpretation in the sutures, those of *P. serpentinus* (Phillips) from the Carboniferous of Yorkshire, England, and Visé, Belgium, are similar to those of *P. monroensis*. The cross section of Phillips species is subangular, however, and its umbilicus is relatively small.

The sutures of *P. mixolobus* (Phillips), also from Yorkshire, are like those of the Illinois species except that the fourth lateral lobe is relatively deep and lanceolate. *P. quinquelobus* Kittl from Sarajevo, Yugoslavia, has deeply impressed whorls and seems to be an advanced species of the genus. *P. hesteri* Moore from the B_2 zone at Cowdale Clough, Yorkshire, differs from the Illinois species in that it has broader lateral lobes and a better developed umbilical lobe which centers on the umbilical seam.

Occurrence.—About 1 mile east of Waterloo, near the headwaters of Kopp Creek, NE$\frac{1}{4}$ sec. 30, R. 8 W., T. 2 S., Monroe Co., Illinois.

Repository.—Worthen Collection at Illinois State Geological Survey, 2589 (holotype and two topotypes).

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THE LEPTOCHOERIDAE

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ABSTRACT—The Leptochoeridae, a North American Oligocene mammalian family, is reviewed. The genera, *Leptochoerus*, *Stibarus* and *Nanochoerus*, n. gen., are recognized as valid genera assignable to this family. Each of the recognized species is discussed and, in some cases, redefined in the light of post-descriptive information. Four new species, *Leptochoerus supremus*, *Stibarus yoderensis*, *Nanochoerus elegans*, (type species) and *N. scotti* are described.

INTRODUCTION

THE enigmatic Leptochoeridae have continued to present a problem in both inter- and intrafamily relationships ever since Leidy described *Leptochoerus spectabalis* in 1856 and Cope introduced *Stibarus obtusilobus* in 1873. Isolated teeth, jaw fragments and bits of maxillaries from members of this family are to be found in almost any museum with a collection of White River fossils. The following report is an attempt to gather together the available information on the known members of this group under one cover, and to establish a basis for identification based on an analysis of the various types and specimens available in our national museums. One immediate point of interest brought out by this study is that the Leptochoeridae are not a rare group of animals but actually quite a common element in the White River fauna.

My thanks are due to Messrs. E. C. Galbreath, J. T. Gregory, G. L. Jepsen, LeRoy Kay, P. O. McGrew, Bryan Patterson, H. G. Roberts, Bobb Schaeffer, G. G. Simpson, R. W. Wilson, A. E. Wood and particularly C. B. Schultz for making available to me specimens and information regarding various specimens, types and localities. The drawings were made by Orla Peters of Oral, South Dakota; the photographs by the author. All measurements, unless otherwise noted, were made with the same instrument and by the author. If they are in error, the errors at least should be consistent.

The following abbreviations are used to designate the institutions to which the various specimens mentioned in the text belong:

AM—Amherst College Museum.
AMNH—American Museum of Natural History.
ANSP—Academy of Natural Sciences of Philadelphia.
CM—Carnegie Museum.
CNM—Chicago Natural History Museum.
SDSM—South Dakota School of Mines and Technology Museum of Geology.
UCM—University of Colorado Museum.
UKMNH—University of Kansas, Museum of Natural History.
UNSM—University of Nebraska State Museum.
USNM—United States National Museum.
YPM—Yale Peabody Museum.

The measurements given in the tables of measurements are the maximum for the directions indicated. Abbreviations used in tables: ant = anterior, post = posterior, tr = transverse, l-b ratio = length-breadth ratio, diam = diameter.

THE FAMILY LEPTOCHOERIDAE

The leptochoerids may be loosely defined as the small Oligocene North American bunodont artiodactyls which basically resemble the primitive Eocene dichobunids, except that the M_2^2 and M_3^3 are smaller than M_1^1. The family status is generally recognized and supported by the lack of later Eocene relatives. It may be that this family actually should be considered a subfamily of the Dichobunidae, but, on the strength of the apparent temporal hiatus between the lepochoerids and the primitive

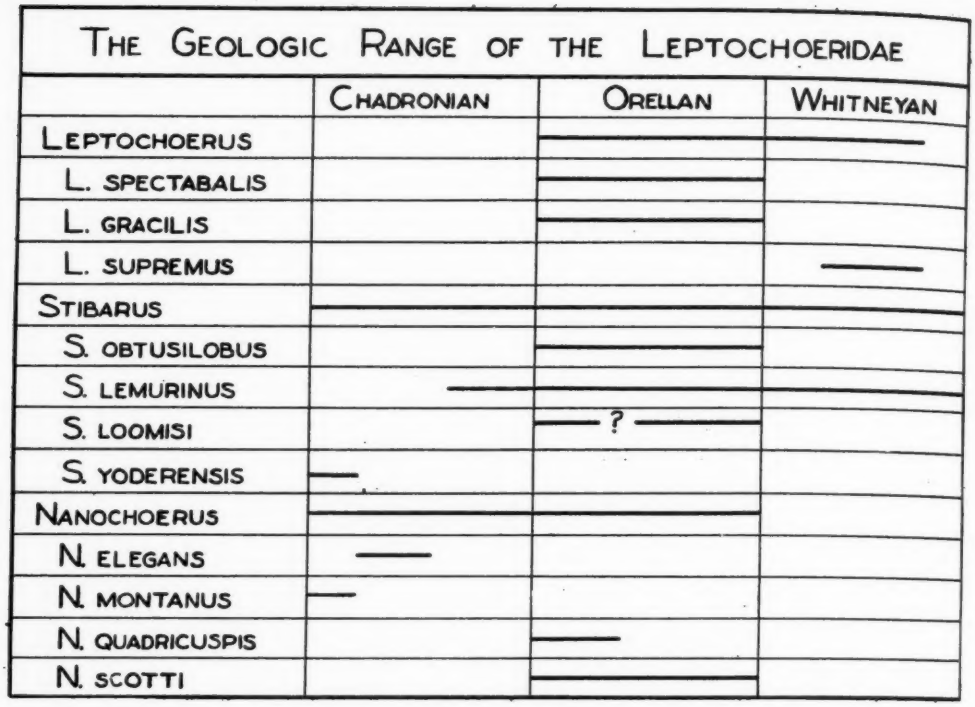


FIG. 1.

dichobunids and the rearward reduction in size of the molars, it is deemed prudent to retain the family in its present recognized status.

THE GENERA OF LEPTOCHOERIDAE

In his monumental work, "The Extinct Mammalian Fauna of Dakota and Nebraska", Leidy (1869) expanded his description of *Leptochoerus spectabalis* Leidy (1856). He based his original description on a jaw fragment (ANSP 15593) collected by F. V. Hayden who found it while working in "the Mauvaises Terres of White River." Leidy states that this was, "Among the specimens of rather uncertain reference . . . ," although he included the genus in the Suidae. Unfortunately, Leidy's type contains only the first and second lower molars; and he stated, "The specimen above described is the only one which could with any degree of certainty be referred to *Leptochoerus spectabalis*." He then continues,

Dr. Hayden's collection of the summer of 1865 contains two additional specimens from the Mauvaises Terres of White River, which appear to be referable to *Leptochoerus spectabalis*. One of them consists of a fragment of the right side of the lower jaw containing the second and third premolars, a portion of the fourth one, and the first true molar. The other specimen is a fragment of the same side of the upper jaw, containing the last premolar and the following pair of true molars.

The type specimen and the referred lower jaw (ANSP 15594) seem to be cospecific on the basis of the single mutual tooth, but there is no sound basis for referring the maxillary to this species. However, it can be referred to the genus *Leptochoerus*.

In 1873 Cope described *Stibarus obtusilobus* based on a jaw fragment (AMNH 6784) containing the P_3. This tooth is characterized by its extreme narrowness, relatively great length, subequal anterior and posterior accessory cusps and additional posterior cingular cusp.

During the same year Cope also described

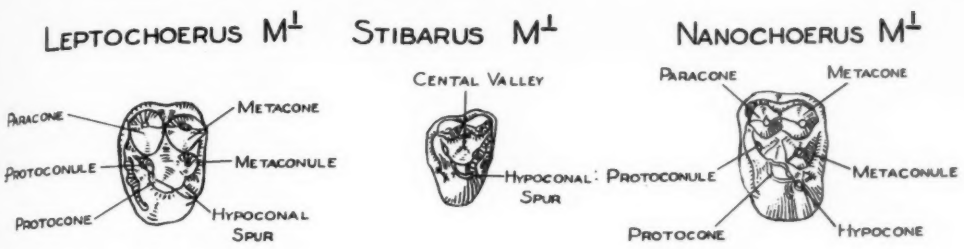


FIG. 2—Occlusal views of the M^1s of the three genera of Leptochoeridae: *Leptochoerus*, *Stibarus*, and *Nanochoerus*. ×2.

Menotherium lemurinum from northeastern Colorado. As this species was based on a jaw fragment with heavily worn dentition, it has generally been ignored or synonymized with either *Leptochoerus* or *Stibarus*.

As the types of the type species of *Leptochoerus* and *Stibarus* have no teeth in common, we must base our distinctions between these two genera on the type of *S. obtusilobus* and the jaw (ANSP 15594) which Leidy referred to *L. spectabalis* in his expanded description of the species. Strictly speaking, *L. spectabalis* could be classed as nomen vanum. Because of the inadequacy of the type, the concept of *Leptochoerus* has been established on the characteristics of the referred lower dentition described in 1869. It would serve no valid purpose to reject the name *Leptochoerus* on this technicality. That being the case, it is expedient to accept the genus as established by Leidy and, as now understood, on the basis of the more nearly complete specimen which Leidy referred to it, figured, and described in his monograph of 1869.

In order to complete the lower cheek tooth series of these two genera, other referred specimens and species must be considered. The first of these is *Leptochoerus gracilis* Marsh (1894) which is based on a partial skull (YPM 10322) containing P_2–M_3 and P^3–M^3. The lower dentition of this specimen indicates that the species is referable to *Leptochoerus* as based on Leidy's referred lower jaw fragment. It was in this publication that Marsh erected the family Leptochoeridae to include Leidy's and his species. *Stibarus montanus* Matthew (1903), based on a jaw fragment (AMNH 9668) with P_2–M_1 has established the concept of *Stibarus* but additional material in the museums of the University of Kansas, the University of Nebraska, and the South Dakota School of Mines and Technology has shown that this species is not referable to *Stibarus*. A partial skull (UNSM 5463) which is referable to *S. lemurinus* gives the best indication of both the upper and lower cheek teeth of this genus.

The characteristics of the lower cheek teeth of the two genera may be tabulated as follows:

	Leptochoerus	*Stibarus*
P_1	Unknown	Unknown
P_2	Tall, single cusp, cingulum complete, posterior cingular cusp present or absent. Length-breadth ratio 2.06–2.33.	Unknown
P_3	like P_2, length-breadth ratio 2.10 or less.	Low, cingulum obscure, strong anterior and posterior accessory cusps, small posterior cingular cusp or trenchant blade, length-breadth ratio >2.8.
P_4	Single cusped, cingulum present, narrower anteriorly than posteriorly.	Cingulum reduced, anterior and posterior lingual accessory cusps present.
M_{1-3}	Without paraconid.	With small paraconid.

KEY TO THE LEPTOCHOERIDAE

	General	P_2	P_3	P_4
Leptochoerus	Upper teeth based on *L. gracilis*, may vary in other species.	Tall, single cusp.	Tall, single cusp.	Single cusp.
L. spectabalis	Upper cheek teeth in text are of questionable reference.	*Principal cusp in center of tooth.[1] *Blades symmetrical. *l-b ratio 2.06.[2]	*Principal cusp in center of tooth. *Blades symmetrical. *l-b ratio 1.90 (1.84–2.05).	
L. gracilis	Only recorded associated upper and lower cheek teeth	*Principal cusp recurved. *Anterior blade convex, posterior blade concave. *l-b ratio 2.33.	*Principal cusp recurved. *Anterior blade convex, posterior blade concave. *l-b ratio 2.00 (1.97–2.09).	*l-b ratio 1.40 (1.40-1.56).
L. supremus	⅓ larger than other species.			
Stibarus	Based on specimens referred to *S. lemurinus* and *S. yoderensis*.		Low, three cusped, sometimes large posterior cingular cusp. l-b ratio >2.80.	Low, three cusped.
S. obtusilobus	Type is only known specimen of certain reference		*Three cusped with well developed cingular cusp. l-b ratio 2.88.	
S. lemurinus	Expanded description based on UNSM 5463.		*No posterior cingular cusp. *l-b ratio 2.91.	*l-b ratio 1.85 (1.78-1.85).
S. loomisi				
S. yoderensis			l-b ratio 2.88. Short "talonid."	
Nanochoerus	Low, three cusped.	Low, three cusped.	Low, three cusped, or bicuspid with smaller posterior cusp	Triangular with small anterior and paired posterior accessory cusps.
N. elegans		*l-b ratio 3.71. *With "talonid" *Anterior and posterior diastema.	*l-b ratio 2.45.	*l-b ratio 1.38–1.47.
N. montanus	Smaller than other species.	*l-b ratio 3.71. *Anterior and posterior diastema. *Without "talonid."	*l-b ratio 2.92.	*l-b ratio 1.57.
N. quadricuspis	Small.			
N. scotti	Teeth massive.		l-b ratio 2.00 Bicuspid with smaller posterior cusp.	*l-b ratio 1.56.

[1] Characters marked with star are found in type specimen.
[2] Length-breadth ratio

KEY TO THE LEPTOCHOERIDAE—*Continued*

Lower Molars	P_2	P_3	Upper Molars
Without paraconid.		Single cusp or with small anterior and posterior accessory cusps and small deuterocone.	No hypocone, semi-isolated protoconule and metaconule.
*M_{1-2} with pronounced interprotoconid-metaconid valley. *Hypoconid connects to metaconid.			
*Shallow, expanded talonid basin.	*Single recurved cusp. *l-b ratio 2.00.	*Single recurved cusp. *l-b ratio 1.40.	*Protoconule and metaconule reduced.
*Very shallow broad talonid basin. *Cusps triangular. *M_3 without attenuated talonid.			
With paraconid.	Three cusps and small posterior cingular cusp.	Three lingual cusps and deuterocone.	Paracone-protocone-metacone form isosceles triangle. Small hypoconal spurs.
			Protoconule-protocone-metaconule ridge very prominent, concave on anterior and posterior sides. Central valley very deep, opens labially between paracone and metacone.
			M^{1-2} with small hypoconal spur. M^3 without hypoconal spur.
	*l-b ratio 3.38.	*l-b ratio 1.58.	*M^{1-2} with hypoconal spur. *Central valley shallow not open labially. *M^{1-2} interrupted cinguli around lingual side of protocone.
Without paraconids.	Low, three cusped.	Four cusped, small deuterocone	M^1 quadritubercular with well developed hypocone.
*Metaconid and protoconid opposite.	*Low, three cusped.		*M^1 with small hypocone.
*Metaconid and protoconid opposite.			
			*M^{1-2} with well developed hypocones.
*Metaconid and protoconid opposite.	*l-b ratio 3.06–3.21. *Low, three cusped.	*l-b ratio 1.59.	*M^1 with well developed hypocone. *M^2 hypoconal spur. *M^1 small mesostyle.

The upper cheek teeth of these genera may be correlated on the basis of the type of *Leptochoerus gracilis* Marsh (YPM 10322) a maxillary (KUMNH 9226), the fragmentary skull (UNSM 5463) which was mentioned above, and a palate from the Yoder member of the Chadron formation in eastern Wyoming (SDSM 5310).

	Leptochoerus	*Stibarus*
	Canine—Unknown	Simple, slightly recurved, laterally compressed cone.
P^2	Simple recurved cusp.	Low, long laterally compressed, with anterior and posterior accessory cusps and minute posterior cingular cusp.
P^3	One cusp, reduced cingulum or small anterior cingular accessory cusp, small posterior accessory cusp and reduced deuterocone.[1]	Three lingual cusps and small to well developed deuterocone.
P^4	Essentially the same in both genera. Distinguishing characteristics have been suggested, but a study of several specimens will show that these ascribed characteristics are not reliable.	
M^1	No hypocone, with or without hypoconal spur, semi-isolated protoconule and metaconule.	Paracone, metacone, and protocone form isosceles triangle, paracone and metacone well developed, metaconule and protoconule anastomosed to protocone; hypocone slightly developed.
M^2	Similar to M^1	Similar to M^1, hypocone reduced to small spur.
M^3	No hypocone or spur, protoconule and metaconule greatly reduced.	Similar to M^2; protoconule well developed, metaconule undeveloped.

[1] P^3's with small anterior and posterior accessory cusps and reduced deuterocones approach the condition found in *Leptochoerus gracilis* and have a much smaller length-breadth ratio than the P^3's of *Stibarus* and *Nanochoerus*.

Leptochoerus and *Stibarus* are the only two heretofore established genera that are recognized. *Laopithecus* Marsh (1875) is regarded as a synonym of *Leptochoerus; Menotherium* Cope (1873) as a synonym of *Stibarus*. Mathew's *S. montanus* and related species are referred to *Nanochoerus* Macdonald, n. gen., which is described below. The principal characteristics of species referred to the three genera are summarized in the accompanying key chart.

Genus Leptochoerus Leidy

Leptochoerus Leidy. Leidy, 1856, Acad. Nat. Sci. Philadelphia Proc., vol. 8, p. 88.
Laopithecus Marsh. Marsh, 1875. Am. Jour. Sci., ser. 3, vol. 8, p. 240.

Diagnosis.—P_{2-4} tall, single cusped or with small posterior accessory cusps; P^4 single cusp or with greatly reduced anterior and posterior cusps and deuterocone, length-breadth ratio less than in other genera (<2.00). M^{1-3} without hypocones.

Leptochoerus spectabalis Leidy

Leptochoerus spectabalis Leidy. Leidy, 1856, Acad. Nat. Sci. Philadelphia Proc., vol. 8, p. 88. ——, Hayden, 1859, Acad. Nat. Sci. Philadelphia, 1858, p. 157. ——, Leidy, 1869, Acad. Nat. Sci. Philadelphia Journ., vol. 7, p. 197, 386, pl. 21, figs. 14–19. ——, Leidy, 1871, U.S.

Explanation of Plate 46

All figures are unretouched photographs

Fig. *1*—*Leptochoerus gracilis* Marsh, mandible with P_2-M_3, occlusal view. SDSM 291. ×1. (p. 446)

2—*Leptochoerus supremus* Macdonald, n. sp. Type specimen, partial mandible with M_{1-3}, occlusal view. SDSM 4090. ×1. (p. 447)

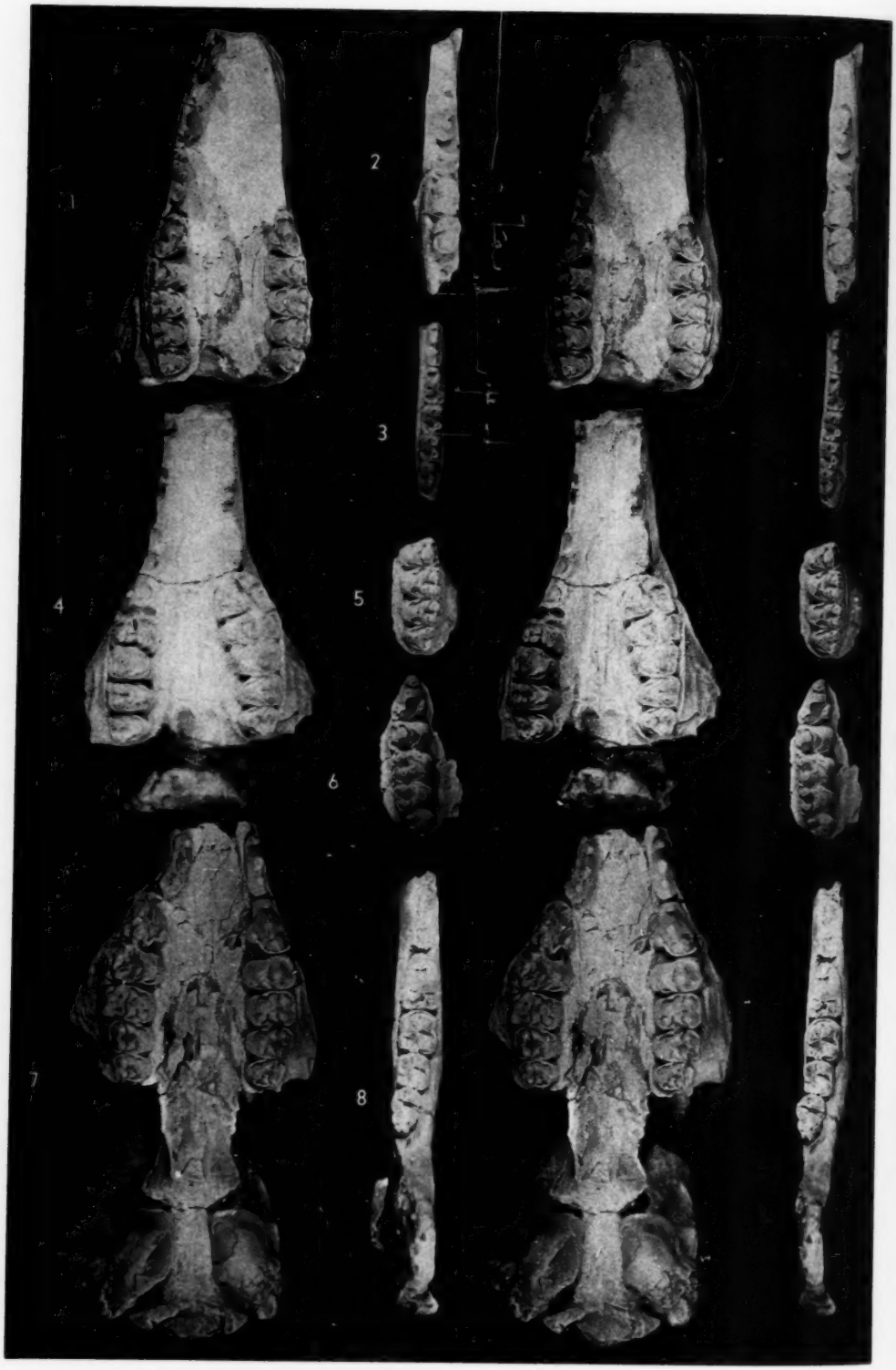
3—*Leptochoerus* sp., left maxillary with P^2-M^3, occlusal view. This form indicates the development of the "*Stibarus*-like" P_3 in some specimens of *Leptochoerus*. KUMNH 9226. ×1. (p. 446)

4—*Nanochoerus quadricuspis* (Hatcher). Type specimen, right maxillary with P^2-M^3, occlusal view. CM 100. ×1. (p. 455)

5—*Nanochoerus* cf. *N. elegans*, partial palate with P_3-M_3, palatal view. SDSM 2639. ×1. (p. 453)

6, 7—*Nanocherus elegans* Macdonald, n. sp. Type specimen, left maxillary with P^2, P^4, and M^1 and lower jaws with P_2-M_3; *6*, maxillary, occlusal view; *7*, lower jaws, occlusal view. AMNH 12315. ×1. (p. 453)

Macdonald, The Leptochoeridae



Macdonald, The Leptochoeridae

Geol. Survey of Montana and portions of adjacent territories; F. V. Hayden, U. S. Geologist, Washington, D. C., 1872, p. 454. ——, KING, 1878, U. S. Geol. Exploration 40th parallel, Clarence King, Geologist in charge, p. 411. ——, GIEBEL, 1888, Bronn's Klass, und Ordn. Bd., 6, Abt. 5, pl. 43, ——, WILCKENS, 1885, Biol. Centralb., Bd. 5, p. 305. ——, ROGER, 1896, Ber. naturwiss. Vereins Schwaben und Neuberg, Abt. 5, Bd. 32, p. 206. ——, MATTHEW, 1899, Am. Mus. Nat. History Bull., vol. 12, p. 59. ——, HAY, 1902, U. S. Geol. Survey Bull. 179, p. 657. ——, TROUESSART, 1905, Catalogus mammalium tam viventium quam fossilium, Quinquale supplementum, p. 656. ——, MATTHEW, 1909, U. S. Geol. Survey Bull. 361, p. 106. ——, O'HARRA, 1910, South Dakota School Mines Bull. 9, pp. 106, 128. ——, COOK, 1912, Nebraska Geol. Survey Bull., vol. 7, p. 37. ——, O'HARRA, 1920, South Dakota School Mines Bull. 13, p. 152. ——, SCOTT, 1940, Am. Philos. Soc. Trans., n.s., vol. 28, pt. 4, p. 368. ——, CAMP, WELLES, & GREEN, 1949, Geol. Soc. America Mem. 37, p. 295. ——, GALBREATH, 1953, Univ. Kansas Paleont. Contrib., Vertebrata, 4, p. 84.

Laopithecus robustus Marsh. MARSH, 1875, Am. Jour. Sci., ser. 3, vol. 9, p. 240. ——, BAIRD, 1876, Ann. Rec. of Sci. Indust., for 1875, p. 336. ——, KING, 1878, U. S. Geol. Exploration 40th parallel, Clarence King, Geologist in charge, p. 411. ——, MARSH, 1893, Am. Jour. Sci., ser. 3, vol. 46, p. 412, pl. 10, fig. 5. ——, ROGER, 1896, Ber. naturwiss. Veriens Schwaben und Neuberg, Abt. 5, Bd. 32, p. 252.

Menotherium lemurinum Cope. TROUESSART, 1897, Catalogus Mammalium tam viventium quam fossilium., p. 72.

Leptochoerus spectabalis LEIDY. MATTHEW, 1899, Am. Mus. Nat. History Bull., vol. 1, p. 357.

Menotherium robustum (Marsh). HAY, 1902, U. S. Geol. Survey Bull. 179, p. 792.

Leptochoerus robustus (Marsh). OSBORN, 1902, Am. Mus. Nat. History Bull., 16, p. 174.

Leptochoerus spectabalis Leidy. TROUESSART, 1905, Catalogus Mammalium tam viventium quam fossilium. Quinquale supplementum, p. 656.

Leptochoerus robustus (Marsh). MATTHEW, 1909, U. S. Geol. Survey Bull., 361, p. 106.

Leptochoerus spectabalis Leidy. SCOTT, 1940, Am. Philos. Soc. Trans., n.s., vol. 28, pt. 4, p. 368.

Type.—Fragment of left ramus with M_{1-2}, ANSP 15593. Type figure: Leidy, 1869, Pl. 21, fig. 16. Also see figs. 17–19. Type locality: "in Mauvaises Terres of White River." Age: Probably Orellan.

Supplemental type.—Fragment of right ramus with P_{2-3} and M_1, ANSP 15594.

Diagnosis.—P_{2-3} with principal cusp in middle of tooth, anterior and posterior blades nearly symmetrical. P_3 with anterior cingular cusp. M_{1-2} with pronounced interprotoconid-metaconid valley; hypoconid connects to metaconid. Length-breadth ratios: P_2, 2.06; P_3, 1.90; P_4, ?1.405.

Remarks.—As noted above, the more nearly complete jaw (ANSP 15594) which Leidy referred to this species in his monograph of 1869 is herein included in the diagnosis of the species and designated as a supplemental type. While the purist will object to this procedure, I believe it is more practical to consider this jaw as a supplemental type rather than to name a new species based on this more nearly complete specimen.

Although Leidy referred the maxillary fragment, ANSP 15595, to this species there is no certainty of association.

The following list of measurements includes two specimens from the Orellan that may be referred to this species. One of these SDSM 262, has a small length-breadth ratio for the P_4 but otherwise seems to be referable to *L. spectabalis*. The jaw fragment (YPM 11799) which Marsh (1875) made the type of *Laopithecus robustus* is probably from the middle Oligocene of South Dakota.

EXPLANATION OF PLATE 47

All figures unretouched photographs

FIG. *1, 2*—*Stibarus yoderensis* Macdonald, n. sp. *1*, Type specimen, partial palate with Canine–M^3, palatal view. SDSM 5310. ×1. *2*, Referred specimen, left mandible with P_3–M_2, occlusal view. SDSM 5315. ×1. (p. 451)

3, 5, 6—*Stibarus lemurinus* (Cope). *3*, Right mandible with P_3–M_3, occlusal view. UNSM 5463. ×1. *5*, Maxillary with P^4–M^3, occlusal view. UNSM 5463, ×1. *6*, Maxillary with P^3–M^3, occlusal view. KUMNH 9225. ×1. (p. 449)

4—*Stibarus loomisi* Scott, Type specimen, partial cranium with Canine, P^1, P^3–M^3, palatal view. AM 1787. ×1. (p. 449)

7, 8—*Nanochoerus scotti* Macdonald, n. sp. Type specimen, cranium and right mandible with P^3–M^3 and P_4–M_3; *7*, cranium, palatal view; *8*, mandible, occlusal view. SDSM 3375. ×1. (p. 456)

Measurements in millimeters

		Type ANSP 15593	ANSP 15594	SDSM 262	UNSM 5467	YPM 11799[1]
P_2	ant-post diam		6.2	7.3	5.8	
P_2	tr diam		3.0	3.1	2.5	
P_2	l-b ratio		2.06	2.35	2.32	
P_3	ant-post diam		7.8	8.5	7.6	
P_3	tr diam		4.1	4.6	3.7	
P_3	l-b ratio		1.90	1.84	2.05	
P_4	ant-post diam		7.25[2]	6.9	7.0	
P_4	tr diam		5.16[2]	5.9	4.9	
P_4	l-b ratio		?1.405	1.16	1.42	
M_1	ant-post diam	5.8	5.5	5.7	5.6	6.7
M_1	tr diam	5.1	5.2	5.1	4.8	5.8
M_2	ant-post diam	4.8		4.7	4.6	5.2
M_2	tr diam	4.5		4.6	4.3	4.9
M_3	ant-post diam				4.8	
M_3	tr diam				3.6	

[1] Type of *Laopithecus robustus* Marsh, courtesy of J. T. Gregory.
[2] Scott's (1940) estimate.

LEPTOCHOERUS sp.
Pl. 46, fig. 3; Text-fig. 3

Leptochoerus spectabilis Leidy. GALBREATH, 1953, Univ. Kansas Paleont. Contrib., Vertebrata, art. 4, p. 84.

Galbreath referred a maxillary (KUMNH 9226) from the middle Oligocene of Northeastern Colorado to *L. spectabalis*. The P^2 and the molars are of the *Leptochoerus* type as seen in *L. gracilis* but the P^3 has a small accessory anterior and posterior cusp as well as a reduced deuterocone. While this specimen cannot be definitely referred to *L. spectabalis*, the measurements are given below as it represents a *Leptochoerus* with a modified *Stibarus* type P^3.

Measurements in millimeters

		KUMNH 9226
P^2	ant-post diam	7.8
P^2	tr diam	3.6
P^2	l-b ratio	2.16
P^3	ant-post diam	8.2
P^3	tr diam	6.9
P^3	l-b ratio	1.18
P^4	ant-post diam	5.5
P^4	tr diam	8.4
M^1	ant-post diam	4.8
M^1	tr diam	7.5
M^2	ant-post diam	4.5
M^2	tr diam	6.7
M^3	ant-post diam	3.7
M^3	tr diam	4.6

LEPTOCHOERUS GRACILIS Marsh
Pl. 46, fig. 1

Leptochoerus gracilis Marsh. MARSH, 1894, Am. Jour. Sci., ser. 3, vol. 48, p. 272, figs. 29, 30. ——, ROGER, 1896, Ber. naturwiss. Vereins Schwaben und Neuberg, Abt. 5, Bd. 32, p. 206. ——, MATTHEW, 1899, Am. Mus. Nat. History Bull., vol. 12, p. 60. ——, MATTHEW, 1901, Am. Mus. Nat. History Mem. 1, p. 443. ——, HATCHER, 1901. Annals Carnegie Mus., vol. 1, p. 131, pl. 1, fig. 4. ——, HAY, 1902, U. S. Geol. Survey Bull. 179, p. 657. ——, MATTHEW, 1909, U. S. Geol. Survey Bull. 361, p. 106. ——, COOK, 1912, Nebraska Geol. Survey, Bull. 7,

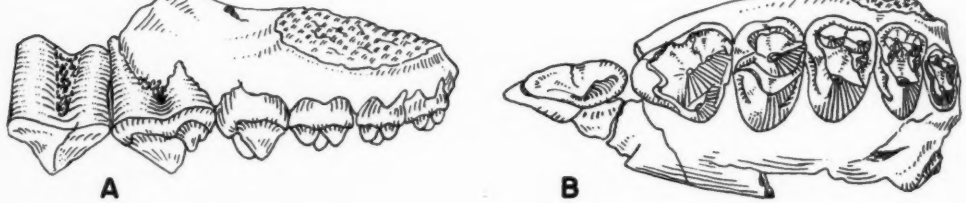


FIG. 3—*Leptochoerus* sp., left maxillary with P^2-M^3; A, labial view; B, occlusal view. KUMNH 9226. ×1.7.

p. 37. ——, O'HARRA, 1920, South Dakota School Mines Bull. 13, p. 152. ——, HAY, 1930, Carnegie Inst. Washington, Pub. 390, vol. 2, p. 752. ——, SCOTT, 1940, Am. Philos. Soc. Trans., vol. 28, (pt. 4), p. 369. ——, SCOTT, 1941, Am. Philos. Soc. Trans., vol. 28, pt. 5, pl. 100, fig. 2. ——, CAMP, WELLES & GREEN, 1949, Geol. Soc. America Mem. 37, p. 295.

Type.—Partial skull, YPM 10322. Type figure: Marsh, 1894, figs. 29 and 30. Also figured in Scott, 1941, Plate 100, fig. 2. Type locality: Cottonwood Creek, South Dakota. Age: Probably Orellan.

Diagnosis.—P_{2-3} with principal cusp recurved; anterior blade convex, posterior blade concave; long "talonid." Lower molars with open shallow talonid basins; protoconid and metaconid opposite; protoconule and metaconule reduced. Length-breadth ratios: P_2, 2.33; P_3, 2.00; P_4, 1.40; P^2, 2.00; P^3, 1.40.

Measurements in millimeters

	Type YPM 10322 (After Scott, 1940)	SDSM 291	KUMNH 9228
Upper dentition, length			
P^2-M^3	35.0		
P^2 ant-post diam	6.0		
P^2 tr diam	3.0		
P^2 l-b ratio	2.00		
P^3 ant-post diam	7.0		
P^3 tr diam	5.0		
P^3 l-b ratio	1.40		
P^4 ant-post diam	4.0		
P^4 tr diam	7.0		
M^1 ant-post diam	5.0		
M^1 tr diam	7.0		
M^2 ant-post diam	4.0		
M^2 tr diam	7.0		
M^3 ant-post diam	3.5		
M^3 tr diam	5.5		
Lower dentition, length			
P_2-M_3	40.0	43.4	
P_2 ant-post diam	7.0	7.8	
P_2 tr diam	3.0	3.2	
P_2 l-b ratio	2.33	2.43	
P_3 ant-post diam	8.0	8.8	8.3
P_3 tr diam	4.0	4.2	4.2
P_3 l-b ratio	2.00	2.09	1.97
P_4 ant-post diam	7.0	7.9	7.5
P_4 tr diam	5.0	5.3	4.8
P_4 l-b ratio	1.40	1.49	1.56
M_1 ant-post diam	6.0	6.1	5.8
M_2 tr diam	5.0	5.0	5.4
M_2 ant-post diam	5.0	5.2	4.8
M_2 tr diam	5.0	4.9	4.7
M_3 ant-post diam	6.0	5.8	5.4
M_3 tr diam	4.0	4.3	3.8

Remarks.—Marsh's type is the only associated skull and jaws of *Leptochoerus* that has been recorded in the literature. As mentioned above, it is our only key to the upper dentition of this genus. In the other species, isolated lower dentitions have been the sole types.

A lower jaw from the South Dakota School of Mines and Technology Museum of Geology (SDSM 291) was referred by Scott (1940) to *Stribarus* sp. (erroneously designated as SDSM 2291) and was figured (Plate 37, figs. 2 and 2a) with a cranium (SDSM 3375) which, with its own mandible, is designated below as the type of *Nanochoerus scotti* Macdonald, n. sp. This jaw (SDSM 291) should be referred to *Leptochoerus gracilis*. Scott referred it to *Stribarus* because the premolars have very small posterior accessory cusps. These cusps are not of the *Stribarus* type but are simply small cuspules which do not greatly modify the basic *L. gracilis* aspect of the specimen.

LEPTOCHOERUS SUPREMUS Macdonald, n. sp.
Pl. 46, fig. 2; Text-Fig. 4

Type.—Fragmentary pair of mandibles with M_{1-3}, SDSM 4090. Paratype: Fragmentary mandible with M_{2-3}, SDSM 409. Type locality: *Protoceras* channel sandstones, 7 miles east of Rockyford, Shannon County, South Dakota. Age: Whitneyan.

Diagnosis.—Molars one-third larger than other described species; talonid basin very shallow, open; hypoconulid and entoconulid form low ridge; cusps triangular; M_3 similar to M_1 and M_2, talonid reduced.

Description.—M_3 with metaconid and protoconid opposite; triangular sulcus anterior to and between protoconid and metaconid; hypoconid triangular, loosely connected to protoconid; hypoconulid and entoconid greatly reduced, forming low ridge at posterior lingual corner; postmetaconid valley widely open lingually; anterior cingulum only. M_2 similar to M_3; larger; hypoconulid and entoconid relatively larger, almost completely enclose talonid basin. M_1 similar to M_2; entoconid and hypoconid relatively larger, completely enclose talonid basin.

Discussion.—While considerably larger than the other known members of this family, this species shows a possible incipient

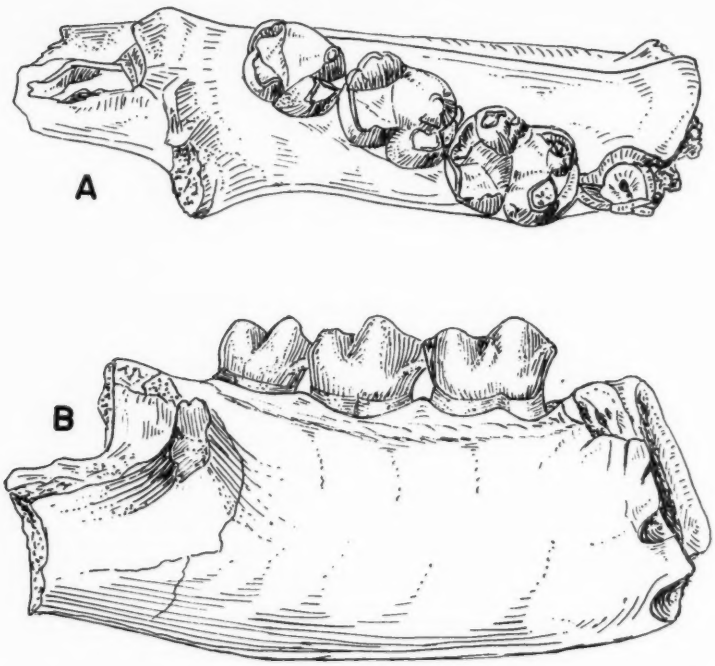


FIG. 4—*Leptochoerus supremus* Macdonald, n. sp. Type specimen, right mandible with M_{1-3}; A, occlusal view; B, labial view. SDSM 4090. ×2.

trend toward tooth reduction. The M_3 has completely lost the attenuated talonid of the other species and closely resembles the anterior molars. The general conformation of the molars suggests that this form has been derived from *Leptochoerus gracilis* Marsh.

Measurements in millimeters

		SDSM 4090 Left	SDSM 4090 Right	SDSM 409
M_1	ant-post diam	8.5	8.5	
M_1	tr diam	6.6	6.5	
M_2	ant-post diam	8.1	7.8	7.7
M_2	tr diam	6.4	6.4	6.2
M_3	ant-post diam	6.2	6.2	6.0
M_3	tr diam	6.0	4.8	4.7
M_{1-3}	total length	22.7	22.5	

Genus STIBARUS Cope

Stibarus Cope. COPE. 1873, Paleont. Bull., vol. 16, p. 3.
Menotherium Cope. COPE, 1874, Acad. Nat. Sci. Philadelphia Proc. 1873, p. 419.

Type species.—*Stibarus obtusilobus* Cope.
Emended diagnosis.—Anterior premolars elongate, low and with three cusps and a small posterior cingular cuspule; lower molars with paraconid; upper molars tritubercular, metaconules and protoconules anastomosed to protocones to form V-shaped ridge, hypocone represented by small spur.

Discussion.—As indicated in the discussion of the genera of leptochoerids, the concept of *Stibarus* has been based primarily on the specimen which Matthew (1903) described as *Stibarus montanus*. Additional material collected since that time has indicated that the species *S. montanus*, is not referable to *Stibarus* but to *Nanochoerus* Macdonald, n. gen., which will be described in a later portion of this report.

STIBARUS OBTUSILOBUS Cope

Stibarus obtusilobus Cope. COPE, 1873, Palaeont. Bull., vol. 16, p. 3. ——, COPE, 1873, Synopsis of new Vertebrata from the Tertiary of Colorado, obtained during the summer of 1873, p. 9. ——, COPE, 1874, Ann. Rept. Geol. and Geog. Survey Territories for 1873, p. 503. ——, COPE, 1886. Am. Naturalist, vol. 20, p. 618. ——, ROGER, 1896, Ber. naturwiss.

Vereins Schwaben und Neuburg, Abt. 5, Bd. 32, p. 215. ——, TROUESSART, 1898, Catalogus Mammalium tam viventium quam fossilium., p. 840. ——, MATTHEW, 1899, Am. Mus. Nat. History Bull., vol. 12, p. 61. ——, MATTHEW, 1901, Am. Mus. Nat. History Mem. 1, p. 358. ——, HAY, 1902, U. S. Geol. Survey Bull. 197, p. 672. ——, MATTHEW, 1903, Am. Mus. Nat. History Bull., vol. 19, pp. 219, 220, fig. 12. ——, PALACKY, 1903, Zool. Jahrb. Syst., Bd. 18, p. 312. ——, TROUESSART, 1905, Catalogus Mammalium tam viventium quam fossilium, Quinquinale supplementum, p. 684. ——, MATTHEW, 1909, U. S. Geol. Surv. Bull. 361, p. 106. ——, SCOTT, 1940, Am. Philos. Soc. Trans., (n.s.), vol. 28, pt. 4, p. 374. ——, CAMP, WELLES, & GREEN, 1949, Geol. Soc. America Mem. 37, p. 335. ——, GALBREATH, 1953, Univ. Kansas. Paleont. Contrib., Vertebrata, art. 4, p. 84.

Type.—Fragment of ramus with P_3. AMNH 6784. Type figure: Matthew, 1903, fig. 12. Type locality: Cedar Creek, Colorado. Age: Orellan.

Diagnosis.—P_3 with principal cusp slightly anterior to middle of tooth; anterior accessory cusp slightly larger than posterior; prominent posterior cingular cusp; length-breadth ratio 2.88; greatest anteroposterior diameter 7.2 mm.; greatest transverse diameter 2.5 mm.

Discussion.—The position of this species with regard to the other species of this genus is unknown; it is unique in that there is no record of another specimen that can with all certainty be referred to this species. This species also represents another of those unfortunate cases of the selection of a poor specimen to be the type of a species. To compound the difficulty this species is also the type of the genus.

STIBARUS LEMURINUS (Cope)
Pl. 47, figs. 3, 5, 6; Text-fig. 5

Menotherium lemurinum Cope. COPE, 1874, Acad. Nat. Sci. Philadelphia Proc. 1873, p. 419. ——, COPE, 1874, Ann. Rept. Geol. and Geog. Survey Territories for 1873, p. 510. ——, COPE, 1874, U. S. Geol. and Geog. Survey Territories, Bull. 1, ser. 1, p. 22. ——, Cope, 1883, Rept. U. S. Geol. Survey Territories, F. V. Hayden, U. S. Geologist in charge, 1884, p. 808, pl. 66, figs. 34–36. ——, TROUESSART, 1897, Catalogus Mammalium tam viventium quam fossilium. Nove editio., p. 72.
Leptochoerus lemurinus (Cope). MATTHEW, 1899, Am. Mus. Nat. History Bull., vol. 12, p. 60. ——, MATTHEW, 1901, Am. Mus. Nat. History, Mem. 1, p. 357.
Menotherium lemurinum Cope. HAY, 1902, U. S. Geol. Survey Bull. 179, p. 792.
Leptochoerus lemurinus (Cope). OSBORN, 1902, Am. Mus. Nat. History Bull., vol. 16, p. 174. ——, TROUESSART, 1905, Catalogus Mammalium tam viventium quam fossilium. Quinquinale supplementum, p. 656. ——, MATTHEW, 1909, U. S. Geol. Survey Bull. 361, p. 106.
Leptochoerus spectabalis Leidy. SCOTT, 1940, Am. Philos. Soc. Trans. (n.s.), vol. 28, pt. 4, p. 368.
Stibarus lemurinus (Cope). GALBREATH, 1953, Univ. Kansas Paleont Contrib., Vertebrata, art. 4, p. 83.

Type.—Partial left mandible with heavily worn P_4-M_3 and alveolus of P_3. AMNH 5349. Type figure: Cope, 1884, pl. 46, figs. 34–36. Type locality: northeastern Colorado. Age?: Orellan, (possibly Chadronian, Galbreath, 1953, personal communication).

Emended diagnosis.—P_3 without posterior cingular cusp, M^{1-2} with hypoconal spurs; protoconule-protocone—metaconule ridge very prominent.

Discussion.—This species may be a synonym of *S. obtusilobus* as has been suggested by previous authors. It is retained as a separate species in this paper as I have seen no other P_3's which have the well developed posterior cingular cusp of *S. obtusilobus.*

A fragmentary skull (USNM 5463) from the University of Nebraska State Museum has a jaw that closely matches the type specimen in size and proportion and also indicates the type of upper dentition possessed by this genus.

Specimens referable to *S. lemurinus* range from early to late Oligocene. In the list below KUMNH 9225 is from the Chadronian, SDSM 537 is from the Whitneyan and the remainder are from the Orellan. There is no doubt but that these actually represent more than a single species, but the available sample is too small to make valid distinctions.

STIBARUS LOOMISI Scott
Pl. 47, fig. 4

?Stibarus loomisi Scott. SCOTT, 1940, Am. Philos. Soc. Trans. (n.s.), vol. 28, pt. 4, p. 376, pl. 36, figs. 2, 2a.
Stibarus loomisi Scott. CAMP, Welles, & GREEN, 1949, Geol. Soc. America Mem. 37, p. 334.

Type.—Anterior portion of cranium with Canine, P^1, P^3-M^3, and alveoli for P^2. AM 1787. Type locality unknown. Age unknown.

Diagnosis.—Larger than *S. lemurinus*, M^2

without hypocone, M^1 with small hypocone.

Discussion.—The dentition of the type of this species is very badly worn. Many of the teeth are broken so that a detailed study of the dentition cannot be made. The lack of a hypocone on M^2, the small hypocone on M^1, and larger size many separate this form from *S. lemurinus*. Scott (1940) recognized that this species possibly could not be referred to *Stibarus* and that it could represent a distinct genus. The dentition shows that this species is referable to the genus *Stibarus* as recognized in this paper.

Measurements in millimeters

	Right	Left
Canine, ant-post diam	2.4	
Canine, tr diam	1.3	
P^1 ant-post diam		4.3
P^1 tr diam		1.7
P^4 ant-post diam	4.2	
P^4 tr diam	6.2	
M^1 ant-post diam	4.2	
M^1 tr diam	6.1	
M^2 ant-post diam	4.4	4.3
M^2 tr diam	6.5	6.4
M^3 ant-post diam	3.8	3.9
M^3 tr diam	5.0	4.8
Total length, Canine—M^3	45.7	
Total length, P^1-M^3		37.4

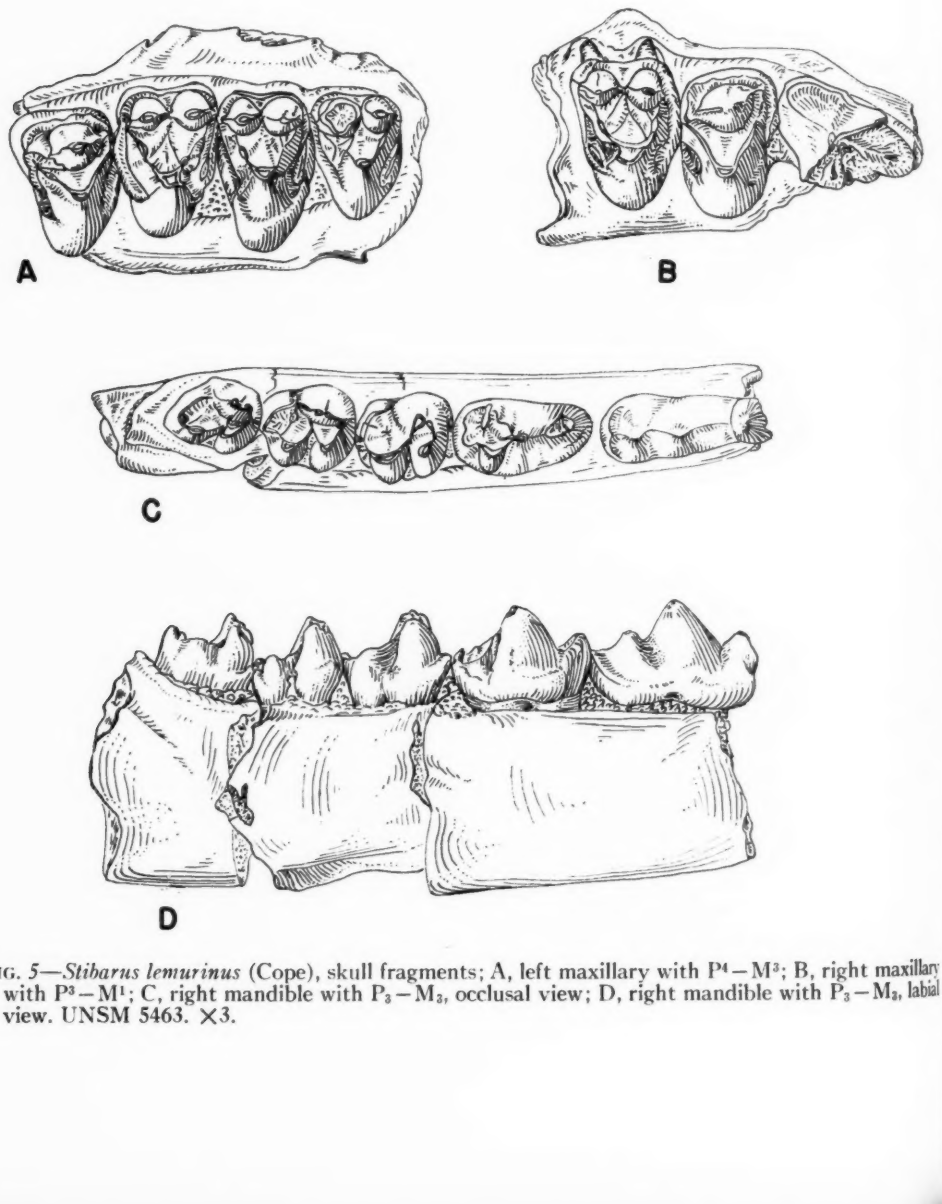


FIG. 5—*Stibarus lemurinus* (Cope), skull fragments; A, left maxillary with P^4-M^3; B, right maxillary with P^3-M^1; C, right mandible with P_3-M_3, occlusal view; D, right mandible with P_3-M_3, labial view. UNSM 5463. ×3.

Measurements in millimeters

	Type AMNH 5349	KUMNH 9231	UCM 19863	SDSM 537	UNSM 5463
P_3 ant-post diam					6.7
P_3 tr diam					2.3
P_3 l-b ratio					2.91
P_4 ant-post diam	5.2		6.1	5.2	5.3
P_4 tr diam	2.8		3.4	2.9	2.9
P_4 l-b ratio	1.85		1.79	1.78	1.82
M_1 ant-post diam	3.7	4.8	4.8	3.9	4.1
M_1 tr diam	3.0	3.7	3.7	3.1	3.4
M_2 ant-post diam	3.7	4.2		3.7	3.9
M_2 tr diam	2.9	3.6		2.8	3.3
M_3 ant-post diam	3.7	4.7			4.1
M_3 tr diam	2.5	3.1			2.6
P_3–M_3 total length					25.2
P_4–M_3 total length	16.8				17.7
M_{1-3} total length	12.0				12.4

	KUMNH 9225	UNSM 5463 Left	UNSM 5463 Right	UNSM 5464 Left	UNSM 5464 Right	UNSM 5465	UNSM 5466
P^2 ant-post diam	7.4						
P^2 tr diam	2.2						
P^2 l-b ratio	3.36						
P^3 ant-post diam	7.0			6.6	6.5		
P^3 tr diam	4.6			4.2	4.1		
P^3 l-b ratio	1.52			1.57	1.58		
P^4 ant-post diam	4.1	3.7	3.8	3.8	4.0	3.9	3.4
P^4 tr diam	6.1	5.35	5.5	5.5	5.5	5.3	4.8
M^1 ant-post diam	4.4	4.1	3.8	3.7	3.7	3.7	3.7
M^1 tr diam	6.0	5.7	5.6	5.4	5.3	5.4	5.3
M^2 ant-post diam	3.7	3.75		3.7	3.7	3.5	3.3
M^2 tr diam	5.7	5.7		5.5	5.5	5.3	5.0
M^3 ant-post diam	3.1	3.3		2.8	2.7	2.8	
M^3 tr diam	4.1	4.2		3.8	3.75	4.1	
P^2–M^3 total length	22.3			20.9	20.8		
P^4–M^3 total length	15.5	15.3		14.8	14.8	14.7	
M^{1-3} total length	11.4	11.4		10.7	10.6	11.7	

STIBARUS YODERENSIS Macdonald, n. sp.
Pl. 47, figs. 1, 2; Text-fig. 6

Type.—Partial palate with C—M^3 SDSM 5310. Type locality: SDSM Yoder Quarry No. 2, sec. 32, T. 23 N., R. 62 W., Goshen County, Wyoming. Age: very early Chadronian.

Referred material.—Fragment of left mandible with P_3, portion of P_4 and M_{1-2}. SDSM 5315.

Diagnosis.—M^{1-3} with hypoconal spur; M^{1-2} with discontinuous lingual cingula; P^4—M^3 with prominent cingula; length-breadth ratios: P^3, 1.58; P^2, 3.38. Central valley of molars not open labially between paracone and metacone.

Description.—M^3 paracone larger than metacone; metaconule larger than protoconule; protocone enlarged posterolingually suggesting hypoconal spur; central valley not open labially between metacone and paracone; cingulum continuous except on posterolingual corner and lingual side of protocone, prominent triangular expansion of cingulum into notch between hypoconal spur and metaconule. M^2 similar to M^3; paracone and metacone subequal; well developed hypoconal spur; minute mesostyle; cingulum interrupted on posterolingual corner of protocone. M^1 similar to M^2; cingulum broken into short segments around base of hypoconal spur and lingual base of protocone. P^4 similar to that of *S. lemurinus;* deuterocone more bulbous, connected more closely to protocone. P^3 with principal cusp tallest in tooth row; posterior accessory cusp smaller and connects to very small posterior cingular cusp; anterior cingular cusp small; well developed deuterocone opposite posterior moiety of principal cusp, separated

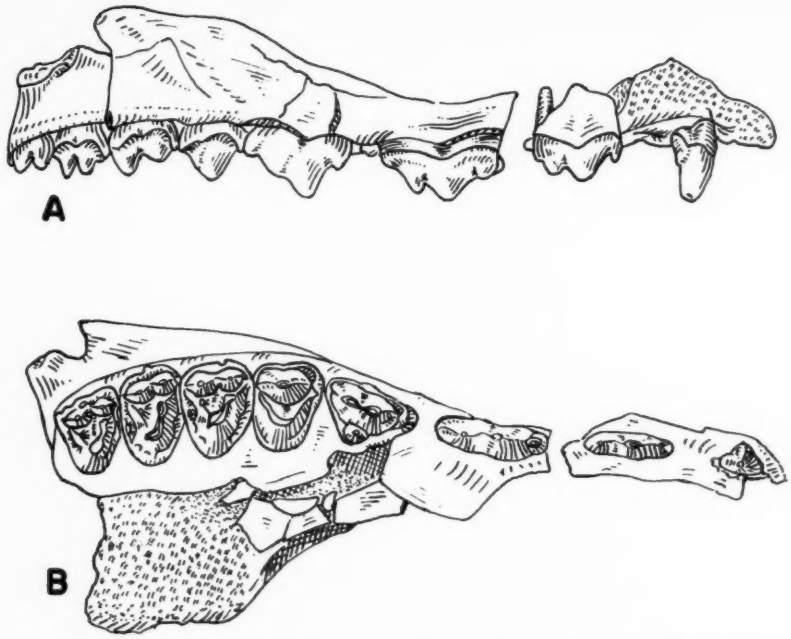


FIG. 6—*Stibarus yoderensis* Macdonald, n. sp. Type specimen, partial palate with Canine–M^3; A, labial view; B, occlusal view. SDSM 5310. ×2.

from principal cusp by deep sulcus; cingulum prominent and continuous except on anterior and labial face of deuterocone and labial anterior face of principal cusp. P^2 separated from P^3 by diastema; three cusps; principal cusp tallest; posterior accessory cusp larger than anterior accessory cusp, extends posteriorly to end of tooth as trenchant blade; no posterior cingular cusp, cingulum indistinct except around posterior moiety of tooth. P^1 separated from P^2 by diastema, similar to P^2 but smaller. Canine separated from P^1 by long diastema, laterally compressed, anterior edge convex, posterior blade straight, apex posterior to center.

Description of referred mandible.—M_{1-2}, badly weathered; apparently similar to that of *S. lemurinus*. P_4 badly weathered; posterior moiety only. P_3 tri-cusped; anterior accessory cusp more widely separated from principal cusp than in *S. lemurinus*. Principal and posterior accessory cusps similar to that of *S. lemurinus;* "talonid" very short; cingulum well developed except around anterior face of anterior accessory cusp.

Discussion.—The molars of *Stibarus yoderensis* are not as specialized as those of *S. lemurinus*. The hypoconal spurs are found on all upper molars, the protocones are broader and partially surrounded by cinguli, and the protoconule-protocone-metaconule ridge is not a prominent feature of the tooth; consequently, this form does not have the deep central valley of the later species.

The badly weathered jaw fragment (SDSM 5315) occludes perfectly with the type specimen; however, it shows a slight amount of wear and while it was found within a few inches of the type it cannot be positively associated with it. The two fragments containing the molars and the posterior portion of the P_4 are heavily weathered while the fragment containing the P_3 is unweathered.

NANOCHOERUS Macdonald, n. gen.

Type species.—*Nanochoerus elegans* Macdonald, n. sp.

Diagnosis.—P_{2-3} low with anterior and posterior accessory cusps; M_{1-3} without paraconids; P^3 with three labial cusps in line

Measurements in millimeters

	Type, 5310 Right	Type, 5310 Left	5315
Canine ant-post diam	2.3		
Canine tr diam	1.4		
P^1 ant-post diam	5.1		
P^1 tr diam	1.4		
P^1 l-b ratio	3.46		
P^2 ant-post diam	7.1		
P^2 tr diam	2.1		
P^2 l-b ratio	3.38		
P^3 ant-post diam	6.5	6.5	
P^3 tr diam	4.1	4.2	
P^3 l-b ratio	1.58	1.54	
P^4 ant-post diam	3.9	4.0	
P^4 tr diam	5.7	5.7	
M^1 ant-post diam	4.5	4.3	
M^1 tr diam	5.9	5.7	
M^2 ant-post diam	4.1	4.3	
M^2 tr diam	5.8	5.9	
M^3 ant-post diam	3.7	3.6	
M^3 tr diam	4.7	4.7	
Length canine—M^3 (estimated)	45.0		
Length P^1–M^3	39.1		
Length P^2–M^3	31.7		
Length P^3–M^3	22.8		
Length P^4–M^3	16.5		
Length M^{1-3}	12.2		
P_3 ant-post diam		7.2	
P_3 tr diam		2.5	
P_3 l-b ratio		2.88	
M_1 ant-post diam		4.9	
M_1 tr diam		3.7	
M_2 ant-post diam		4.5	
M_2 tr diam		3.4	

and well developed deuterocone; M^1 with well developed hypocone, metaconule and protoconule prominent; M^2 hypocone reduced, metaconule and protoconule prominent.

Discussion.—This genus includes those species which, with the exception of *Stibarus obtusilobus*, *S. lemurinus*, and *S. loomisi* have been referred to *Stibarus*. With the discovery of more complete specimens which are referable to *Stibarus lemurinus* it has become evident that Matthew (1903) was in error in referring *Nanochoerus montanus* to *Stibarus*. This assignment established an erroneous concept of *Stibarus* which, while seemingly valid on the basis of the materials then at hand, has since proved to be incorrect.

The following summary of the characteristics of *Nanochoerus* is set in tabular form to conform with the summary given for *Leptochoerus* and *Stibarus* in the earlier discussion of those genera:—

P_1	Unknown.
P_2	Long, low, three cusped, obscure cingulum.
P_3	Long, low, three cusped, well developed posterior cingulum.
P_4	Principal cusp with accessory anterior lingual cusp and lingual and semi-medial posterior accessory cusps.
M_{1-3}	Without paraconid.
P^2	Long, low, three cusped, cingulum obscure.
P^3	Three labial cusps, small deuterocone.
P^4	Essentially as in other genera.
M^1	All cusps including hypocone isolated and well developed.
M^2	Hypocone reduced to spur, protoconule and metaconule reduced.
M^3	No hypocone, protoconule, and metaconule greatly reduced.

NANOCHOERUS ELEGANS Macdonald, n. sp.
Pl. 46, figs. 5–7; Text-fig. 7

Type.—Maxillary with P^2, P^4, M^1, a portion of P^3 and the roots of M^2, and a pair of lower jaws with P_2—M_3 and the alveoli for the canine and P_1. AMNH 12315.[1] Type locality: lower *Oreodon* zone, Quinn Draw Basin, Pennington County, South Dakota. Age: Orellan.

Diagnosis.—Larger than *S. montanus;* diastema between canine and P_1, P_1 and P_2 and P_2 and P_3; length-breadth ratios: P_2, 3.71; P_3, 2.45. M_3 reduced.

Description.—M_3 reduced; protoconid and metaconid opposite, separated by deep sulcus which closes anteriorly and posteriorly; hypoconid connects to lingual edge of protoconid; hypoconulid largest cusp on talonid, separated from entoconid by deep narrow sulcus; anterior cingulum only. M_2 protoconid slightly anterior to metaconid, separated by deep narrow sulcus with closed ends; hypoconid largest talonid cusp, connects to trigonid between protoconid and metaconid, connects to smaller entoconid with very small hypoconulid extending posteriorly on midline; talonid basin opens labially through narrow V-shaped notch, anterior and posterior cingulum with short segment at base of sulcus between protoconid and hypoconid. M_1 similar to M_2; pro-

[1] The type of this species, from the collections of the American Museum of Natural History, is accompanied by a label printed by Albert Thompson. It is marked "*Stibarus*" (in ink) "*elegans* sp. indesc." (in pencil). I suspect that the identification probably was made by W. D. Matthew in anticipation of eventual description. The specimen was loaned for study and description through the courtesy of Dr. G. G. Simpson.

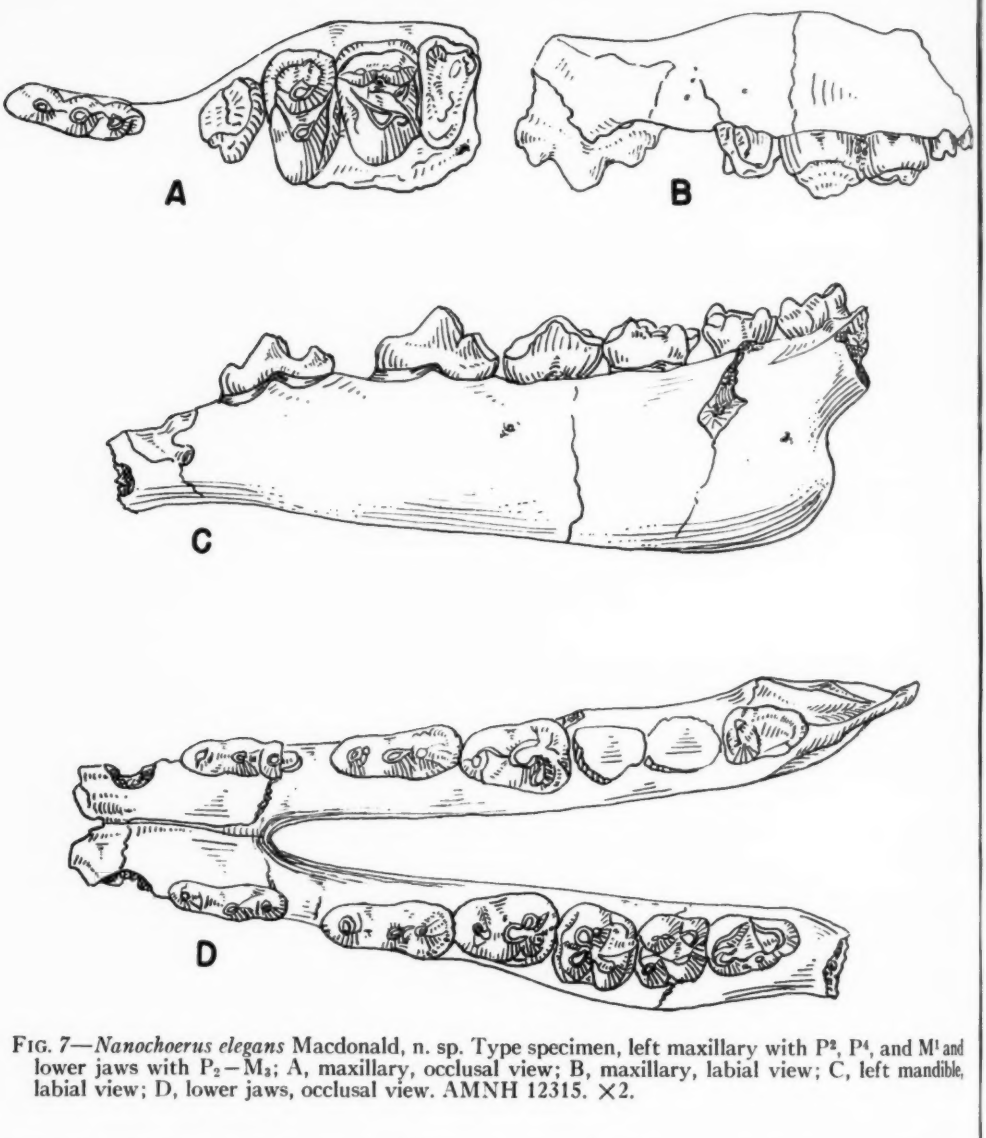


FIG. 7—*Nanochoerus elegans* Macdonald, n. sp. Type specimen, left maxillary with P^2, P^4, and M^1 and lower jaws with P_2-M_3; A, maxillary, occlusal view; B, maxillary, labial view; C, left mandible, labial view; D, lower jaws, occlusal view. AMNH 12315. ×2.

toconid farther forward; hypoconulid larger, extending lingually. P^4 anterior accessory cusp connects to principal cusp labially to midline, compressed antero-posteriorly; two lateral posterior accessory cusps; cingulum continuous but very indistinct. P_3 posterior accessory cusp larger than anterior accessory cusp; two ridges run posteriorly from apex, labial ridge parallels midline and joins cingulum, lingual ridge runs toward posterior lingual corner of tooth but does not reach cingulum; principal cusp tallest in lower cheek tooth series; anterior cusp connects to principal cusp labially of midline; cingulum indistinct except around posterior third of tooth. P_2 separated from P_3 by diastema; three cusped, anterior and posterior cusps subequal. P_1 alveolus only; separated from P_2 by diastema; single rooted. Canine alveolus only; nearly recumbent. Symphysis extends to posterior end of P_2. Mental foramina below midpoint between

P_3 and P_4 and below posterior border of alveolus of P_1. M^1 with prominent labial cingulum; hypocone reduced. P^4 with labial cingulum prominent. P^3 represented by labial posterior cusp only; cingulum prominent. P^2 with subequal anterior and posterior accessory cusps; very small posterior cingular cusp closely attached to posterior accessory cusp.

Discussion.—This species appears to be a direct successor of *Nanochoerus montanus* (Matthew) from the early Oligocene. It has been chosen as the type species of the genus *Nanochoerus* as the type specimen contains a nearly complete lower dentition and associated upper cheek teeth.

Measurements in millimeters

		Type, AMNH 12315 Left	Type, AMNH 12315 Right	SDSM 3356
P_2	ant-post diam	7.8		
P_2	tr diam	2.1		
P_2	l-b ratio	3.71		
P_3	ant-post diam	8.7	8.8	
P_3	tr diam	3.5	3.5	
P_3	l-b ratio	2.48	2.51	
P_4	ant-post diam	6.5	6.8	6.7
P_4	tr diam	4.7	4.6	5.1
P_4	l-b ratio	1.38	1.47	1.31
M_1	ant-post diam	5.8	5.5	
M_1	tr diam	4.8	4.8	
M_2	ant-post diam	4.6		4.4
M_2	tr diam	4.3		4.8
M_3	ant-post diam	4.7	4.7	5.1
M_3	tr diam	3.3	3.2	3.5
P_2–M_3	total length	41.8	41.2	
M_{1-3}	total length	15.6		
P^2	ant-post diam		8.9	
P^2	tr diam		2.5	
P^2	l-b ratio		3.56	
P^4	ant-post diam		4.7	
P^4	tr diam		7.5	
M^1	ant-post diam		4.8	
M^1	tr diam		7.1	

NANOCHOERUS MONTANUS (Matthew)

Stibarus montanus Matthew. MATTHEW, 1903, Amer. Mus. Nat. History Bull., vol. 19, p. 219, fig. 13. ——, TROUESSART, 1905, Catalogus Mammalium tam viventium quam fossilium. Quinquinale supplementum, p. 684. ——, MATTHEW, 1909, U. S. Geol. Survey Bull. 361, p. 104. ——, COOK, 1912. Nebraska Geol. Survey Bull. 7, p. 35. ——, HAY, 1930, Carnegie Inst. Washington Publ. 390, p. 753. ——, RUSSELL, 1936, Royal Soc. Canada Trans., vol. 30, p. 78. ——, SCOTT, 1940, Am. Philos. Soc. Trans. (n.s.), vol. 28, pt. 4, p. 375. ——, CAMP, WELLES, & GREEN, 1949, Geol. Soc. America Mem. 37, p. 335.

Type.—A right lower jaw with P_2–M_1. AMNH 9668. Type figure: Matthew, 1903, fig. 13. Type locality: Pipestone Springs, Jefferson County, Montana. Age: early Chadronian.

Diagnosis and description.—(Matthew, 1903)

> Third premolar with no posterior cingular cusp. The second premolar is long and laterally compressed with three rounded cusps in line, the anterior the smallest, the median the highest. The third premolar has a similar form and composition but the median and posterior cusps are somewhat larger and there is a cingulum around the posterior end of the tooth. The fourth premolar is wider but not much over half as long as the third; it has a main cusp, protoconid, and anterior cusp connected with it by a ridge, a postero-internal and postero-external cusp, all worn off in the specimen and none marginal, and a posterior cingulum. The first molar has four chief cusps, the external ones somewhat crescentic, the postero-internal smaller than the others, and a posterior cingulum with small hypoconid. P_2 with diastema behind and in front of it.

Emended diagnosis.—Small. P_2 with diastema anterior and posterior. Length-breadth ratio of P_2, 3.52; P_3, 29.2; P_4, 1.57.

Remarks.—As mentioned above, this species was assigned to *Stibarus* by Matthew in 1903. I cannot determine whether or not this species had a paraconid, but considering the close relationship that it shows to *Nanochoerus elegans*, it may be presumed that it does not.

Measurements in millimeters

P_2	ant-post diam	6.7
P_2	tr diam	1.9
P_2	l-b ratio	3.52
P_3	ant-post diam	7.3
P_3	tr diam	2.5
P_3	l-b ratio	2.92
P_4	ant-post diam	5.2
P_4	tr diam	3.3
P_4	l-b ratio	1.57
M_1	ant-post diam	4.5
M_1	tr diam	3.9

NANOCHOERUS QUADRICUSPIS (Hatcher)

Pl. 46, fig. 4

Leptochoerus quadricuspis Hatcher. HATCHER, 1901, Annals Carnegie Mus., vol. 1, p. 131, pl. 1, fig. 3.

?Stibarus quadricuspis (Hatcher) MATTHEW, 1903, Am. Mus. Nat. History Bull., vol. 19, p. 230.

Leptochoerus quadricuspis Hatcher. TROUESSART, 1905, Catalogus Mammalium tam viventium

quam fossilium. Quinquinale supplementum, p. 656.

Stibarus quadricuspis (Hatcher). MATTHEW, 1909, U. S. Geol. Survey Bull. 361, p. 106. ——, O'HARRA, 1920, South Dakota School Mines Bull. 13, p. 153. ——, HAY, 1930, Carnegie Inst. Washington Publ. 390, vol. 2, p. 753.

Type.—Right maxillary with P^3-M^3. CM. 100. Type figure: Hatcher, 1901, Pl. 1, fig. 3. Type locality: *Oreodon* beds, Warbonnet Creek, Sioux, Co., Nebraska. Age: Orellan.

Diagnosis.—M^2 with small hypocone; M^1 with well developed hypocone; M^3 with complete cingulum.

Remarks.—This is the only species of *Nanochoerus* based exclusively on an upper dentition. The lower dentitions referred to this species by Hatcher (1901) in his discussion of the species are much too large to belong to *N. quadricuspis*. A pair of partial mandibles (SDSM 3319) from the upper nodular layer (Orellan) on Bear Creek in the South Dakota Badlands occlude perfectly with the teeth of the type specimen. While these mandibles cannot be referred positively to *N. quadricuspis*, their measurements are included as an indication of the size of the lower teeth which would belong to this species. The other two mandibles (ANSP 14849 and 14938) from the Orellan near Scenic, South Dakota, and Hat Creek, Wyoming, although somewhat smaller, are tentatively referred to this species.

NANOCHOERUS SCOTTI Macdonald, n. sp.
Pl. 47, figs. 7, 8; Text-figs. 8, 9

Stibarus obtusilobus Cope. SCOTT, 1940, Am. Philos. Soc. Trans., vol. 28, pt. 4, p. 372, pl. 37, fig. 1; 1941. Ibid. pt. 5, pl. 100, fig. 3.

Type.—Cranium and portion of right mandible with P^2-M^3, P_4-M_3 roots of P_3 and posterior alveolus of P_2. SDSM 3375. Type figure: Scott, 1940, Pl. 37, fig. 1; 1941, pl. 100, fig. 3. Type locality: lower *Oreodon* zone, west side of Cuny Table, Shannon County, South Dakota. Age: Orellan.

Diagnosis.—Teeth larger and more massive than in other species; P_2 appressed to P_3; length-breadth ratio P_4, 1.56; protoconid and metaconid of M_{1-3} not opposite; M^1 with mesostyle.

Description.—M_3 broken; metaconid very tall; reduced protoconid; metaconid and protoconid not opposite; hypoconid connects to metaconid; hypoconid and hypoconulid subequal; entoconid small, partially separated from hypoconulid by small valley; talonid deeply basined, lingual V-shaped opening; no cingulum; with metaconid tallest cusp; slightly posterior to protoconid; hypoconid triangular, connects anteriorly to metaconid, connects posteriorly to small hypoconulid; entoconid and hypoconulid subequal; talonid basin deep, opens lingually through V-shaped notch; cingulum at base of labial notches between protoconid and hypoconid and across posterior end of

Measurements in millimeters

		Type CM100	SDSM 3319 right	SDSM 3319 left	ANSP 14849	ANSP 14938
P^3	ant-post diam	6.8				
P^3	tr diam	5.2				
P^3	ant-post diam	4.1				
P^4	tr diam	6.5				
M^1	ant-post diam	4.7				
M^1	tr diam	6.4				
M^2	ant-post diam	4.1				
M^2	tr diam	6.0				
M^3	ant-post diam	3.4				
M^3	tr diam	4.4				
P_3	ant-post diam			7.9		
P_3	tr diam			3.2		
P_3	l-b ratio			2.46		
P_4	ant-post diam		6.7	6.5	6.1	5.7
P_4	tr diam		3.8	3.8	3.3	3.1
P_4	l-b ratio		1.76	1.71	1.84	1.83
M_1	ant-post diam		4.8	4.6	4.3	4.2
M_1	tr diam		3.8	3.8	3.5	3.3
M_2	ant-post diam		3.9	3.9	3.9	3.8
M_2	tr diam		3.4	3.4	3.4	3.3
M_3	ant-post diam		3.7	3.7	4.5	4.3
M_3	tr diam		2.7	2.8	2.7	2.6

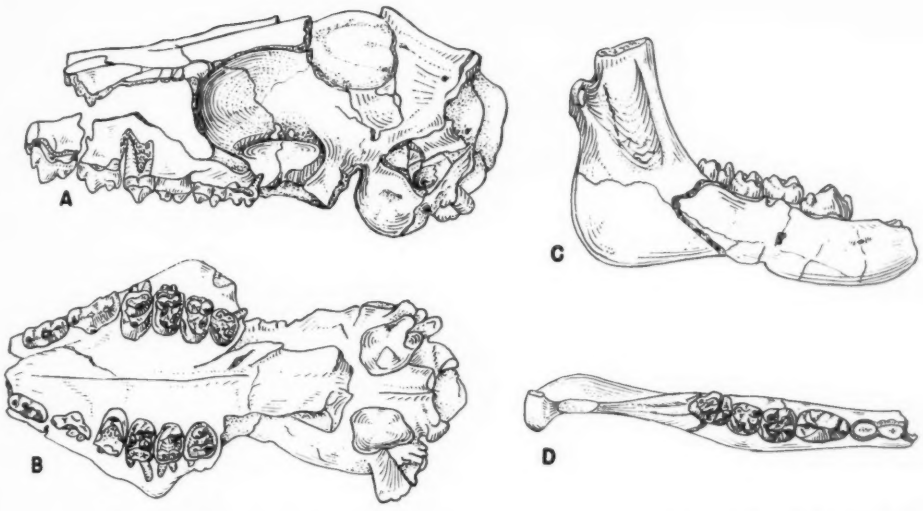


FIG. 8—*Nanochoerus scotti* Macdonald, n. sp. Type specimen, cranium with P^2-M^3 and right mandible with P_4-M_3; A, cranium, lateral view; B, cranium, palatal view; C, right mandible, labial view; D, right mandible, occlusal view. SDSM 3375. ×1.7.

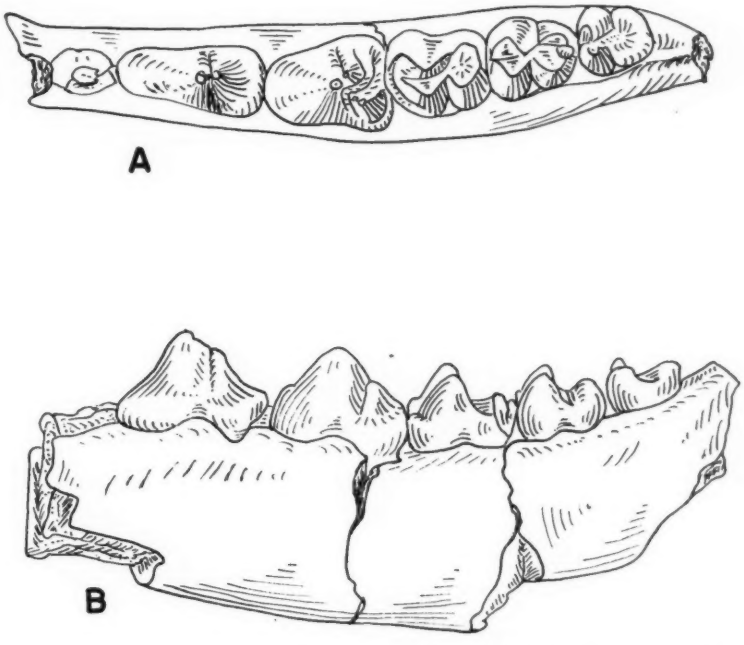


FIG. 9—*Nanochoerus scotti* Macdonald, n. sp., left mandible with P_2-M_3; A, occlusal view; B, labial view. UNSM 5469. ×2.

tooth. M_1 similar to M_2; hypoconid connects more firmly to metaconid; hypoconulid and entoconid subequal; anterior cingulum in addition to M_2 type cingulum. P_4 tapers slightly anteriorly; small round anterior accessory cusp, connects labially to principal cusp; two lateral posterior accessory cusps, with small median ridge running from principal cusp, between posterior or accessory cusps to cingulum; cingulum around posterior end of tooth running from labial posterior accessory cusp to lingual posterior accessory cusp. P_3 roots only appressed to P_4. P_2 posterior portion of posterior alveolus only; tooth would have been appressed to P_3. M^3 much smaller M^2; paracone larger than metacone;protoconule and metaconule subequal; separated from protocone, separated from paracone and metacone by sulci; hypoconal ridge only; cingulum continuous except over lingual side of protocone. M^2 similar to M^3; paracone and metacone subequal; protoconule and metaconule relatively larger; protocone with ridge running from just posterior of apex to cingulum on posterior side, representing rudimentary hypocone; small mesostyle. M^1 quadritubercular with well developed hypocone; well developed mesostyle. P^4 bicuspid as in all leptochoerids; cingulum continuous except on lingual and anterior sides of deuterocone. P^3 four-cusped, three labial cusps in line, posterior cusp taller than anterior cusp and connected to principal cusp by a ridge; principal cusp tallest cusp in cheek tooth row; deuterocone small, slightly posterior of center of principal cusp; cingulum extends from posterior edge of deuterocone around posterior cusp to mid-point between posterior cusps and principal cusp on labial side. P^2 three cusps in line; posterior cusp closely connected to principal cusp as in P^3; anterior cusp smaller, separated from principal cusp; cingulum indistinct, continuous around posterior moiety of tooth.

Remarks.—This specimen was used by Scott (1940) for the basis of his description of the skull and dentition of *Stibarus* and was referred to *S. obtusilobus* Cope. The lower jaw (SDSM 291) which was figured with this cranium is herein referred to *Leptochoerus gracilis* Marsh.

A lower jaw (Text-fig. 9) and maxillary (UNSM 5469) from the Orellan of Nebraska is referable to this species. The P_3 has a modified *Leptochoerus* pattern with a strong central cusp and a smaller closely connected posterior cusp. The anterior blade of the principal cusp and the posterior blade of the secondary cusp are concave. The widest part of the tooth is just below the center of the posterior cusp.

The P_3 indicates that this species is not closely related to either *N. montanus* or *N. elegans*, as these two species have P_3's resembling that found in *Stibarus*. On the other hand the upper molars suggest that this species may be closely related to *N. quadricuspis*.

Measurements in millimeters

		Type SDSM 3375 Right	Type SDSM 3375 Left	UNSM 5469
P^2	ant-post diam	9.0	9.2	
P^2	tr diam	2.8	3.0	
P^2	l-b ratio	3.21	3.06	
P^3	ant-post diam		8.6	8.3
P^3	tr diam		5.4	6.1
P^3	l-b ratio		1.59	1.36
P^4	ant-post diam		5.5	4.8
P^4	tr diam		7.6	8.2
M^1	ant-post diam		5.0	5.0
M^1	tr diam		7.2	7.5
M^2	ant-post diam	4.7	4.7	4.7
M^2	tr diam	6.7	6.7	6.8
M^3	ant-post diam	3.8		3.8
M^3	tr diam	5.2		5.3
P^2–M^3	total length	37.2	37.3	
M^{1-3}	total length		14.3	14.6
P_3	ant-post diam			8.8
P_3	tr diam			4.4
P_3	l-b ratio			2.00
P_4	ant-post diam	7.8		7.4
P_4	tr diam	5.0		5.4
P_4	l-b ratio	1.56		1.37
M_1	ant-post diam	5.8		5.7
M_1	tr diam	5.3		4.8
M_2	ant-post diam	4.8		4.7
M_2	tr diam	4.5		4.8
M_3	ant-post diam	6.0		4.7
M_3	tr diam	3.5		3.5
P_3–M_3	total length			31.8
P_4–M_3	total length	25.6		23.2
M_{1-3}	total length	17.4		15.4

ORIGIN OF THE LEPTOCHOERIDAE

Scott (1940) makes no definite statement as to his views on the origin of the Leptochoeridae. On page 378 he says,

> The origin of the family geographically is yet obscure and uncertain; it would seem, on the whole, most probable that *Leptochoerus* and *Stibarus* were derived from such Bridger ancestors as *Helohyus*, but the scanty and, frag-

mentary material, as yet available, is insufficient for any assured conclusions, and the failure to find any trace of the Leptochoeridae in the Uinta may not be significant, in view of the rarity of these fossils and the evident incompleteness of the Uinta faunal list, as we now have it. On the other hand, it is quite possible that these genera were of Old World origin and were among the many immigrant forms which entered North America in the Early Oligocene. Even in the White River beds, they are among the rarest of finds and after more than eighty years since Leidy's first description, our knowledge of the group remains extremely incomplete. No trace of it has been found in any formation later than the White River.

A study of the more nearly complete and more extensive material now available does not clarify the situation. A tabulation of dental characters (an admittedly inadequate approach) between the early Eocene bunodont artiodactyls and the leptochoerids does little to solve the problem. In general the lower premolars seem to resemble the *Leptochoerus* type. The lower molars usually have a paraconid as in *Stibarus* although some are similar to *Leptochoerus*. The upper premolars resemble those of *Leptochoerus*. The upper molars either resemble *Leptochoerus*, as in the case of *Diacodexis*, or else have hypocones which are either more or less prominent than in *Nanochoerus*.

This confusing admixture of primitive and advanced characteristics raises the question of a polyphyletic origin for the Leptochoeridae. In spite of the shared characteristic of rearward reduction of size in the molars the leptochoerids may not be a single family but rather survivors of three different lines of Eocene dichobunids.

MANUSCRIPT RECEIVED MARCH 29, 1954

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JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 460–461, PLS. 48–49, MAY 1955

GALLATINOSPONGIA, A NEW SILICEOUS SPONGE FROM THE UPPER CAMBRIAN OF WYOMING

VLADIMIR J. OKULITCH AND WALLACE G. BELL
University of British Columbia and University of Wyoming

ABSTRACT—A new genus and species of siliceous sponge, *Gallatinospongia conica*, is described from the upper limestone member of the Gallatin formation (Upper Cambrian) on the southeast flank of the Wind River Mountains in central Wyoming. It occurs just above faunas characteristic of the *Prosaukia-Ptychaspis* zone.

INTRODUCTION

THE sponge described in this paper was discovered by the junior author in 1949 in the upper part of the Gallatin formation (Upper Cambrian) at Beaver Creek Canyon on the southeast flank of the Wind River Mountains in Fremont County, Wyoming. He returned to the locality in 1953 and found several more specimens which were turned over to the senior author for study and description.

All the specimens have come from a single bed 294 feet above the base of the Gallatin formation (170 feet above the base of the upper limestone member as recognized by Miller, 1936) in the NE¼ NE¼ sec. 1, T. 29 N., R. 98 W. (Locality 2998/1A in the University of Wyoming files). From the junior author's collection, Dr. Alan B. Shaw of the University of Wyoming has identified the following (distances measured stratigraphically below the sponge bed; UW = University of Wyoming):

Dikelocephalid remains, UW IT-314, 10 feet
Syntrophina? primordialis, UW IT-321, 34 feet
Dartonaspis cf. *D. knighti* and *Multivasculatus ovatus*, UW IT 319, in float, 34 feet
Ptychaspis pygidium, UW IT-322, 59 feet
Dicellomus mosaicus, UW IT-323, 82 feet
Taenicephalus cordillerensis, UW IT-313, 136 feet
Billingsella sp. and *Ocnerorthis cooperi*, UW IT-316–318, 146 feet
Elvinia tetonensis, UW IT-320, 165 feet

From this evidence, Shaw concludes that the stratum which yielded the sponges is younger than the *Prosaukia-Ptychaspis* zone of the Franconian.

SYSTEMATIC DESCRIPTIONS

Genus GALLATINOSPONGIA Okulitch and Bell, n. gen.

Type species: *Gallatinospongia conica* Okulitch and Bell, n. sp.

Conical sponges with thin walls perforated by transverse and longitudinal canals. The transverse canals are in the outer portion of the wall, the longitudinal canals in the inner portion. Spongocoel wide. Walls made of felted fibrous and loose monoaxial spicules which line the canals and lacunae. Hexactinal spicules have not been observed, and it is the writers' opinion that the sponge should be referred to the Class Desmospongia, and possibly to the Order Monaxonida. The sponge superficially resembles

EXPLANATION OF PLATE 48

FIGS. *1–3*—*Gallatinospongia conica* Okulitch and Bell, n. gen., n. sp. *1*, transverse polished section, ×1.5, showing transverse radial canals in the outer portion of the wall; *2*, longitudinal polished section, ×1.5, showing the conical shape and the general characteristics of the wall; *3*, transverse thin section, ×3, showing vertical canals or lacunae in the inner portion of the wall (lower, left hand corner). All figures are of the holotype, U.B.C. C 108. (p. 461)

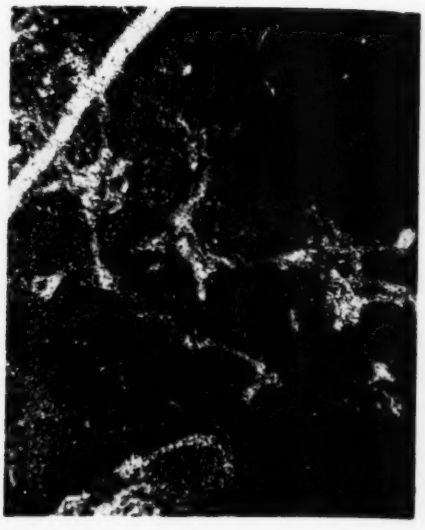
1

2

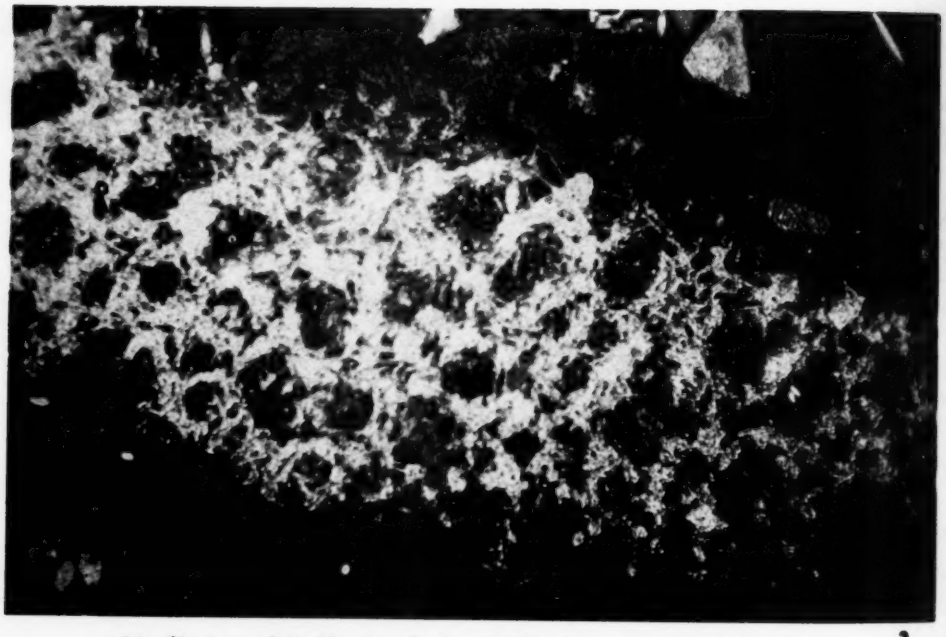
3

Okulitch and Bell, Cambrian *Gallatinospongia*, Wyoming

1



2



3

Okulitch and Bell, Cambrian *Gallatinospongia*, Wyoming

Archaeoscyphia minganensis (Billings) but differs from it in the possession of longitudinal canals in the part of the wall adjacent to the spongocoel, and much finer, almost fibrous spicules.

GALLATINOSPONGIA CONICA Okulitch and Bell, n. sp.

Pl. 48, figs. 1–3; Pl. 49, figs. 1–3

A conical sponge with an apical angle of about 50 degrees, elliptical in cross section. The best specimen measures about 40 mm. in both diameter and height. A larger but less perfect specimen is 45 mm. in diameter. Both specimens were originally slightly larger, but grinding and polishing have reduced the size somewhat. The wall is relatively thin, about 5 mm. across. The outer portion of the wall shows radial canals; the inner portion shows rounded or elongate lacunae which probably were longitudinal canals paralleling the wall. The central cavity is of exceptionally great diameter, about six times the wall thickness, and is free from all skeletal matter.

The canals and lacunae are surrounded by skeletal elements consisting of semi-isolated calcitic spicules, felted spicules, and calcitic masses. The latter undoubtedly were originally spicular, but recrystallization has obliterated clear outlines and merged the spicules into patches of crystalline calcite. It is the writers' belief, based upon the shape of the spicules, that the spicules were originally siliceous; but during the process of fossilization, the silica was removed and replaced by calcite. Such replacement has been observed by Hinde (1887–1893, p. 58) who said

> on the other hand where the calcite has infilled the molds formed in a matrix of chalcedonic silica, the replaced skeleton presents all the details of the original skeleton, with such even and clearly defined outlines that it has been mistaken for the original substance of the skeleton, and the sponge has been described as calcareous.

Some of the spicules are distinctly monaxons; but a great many are thin and threadlike, forming felted aggregates. Some have a tendency to have paired rays, as in triradiate spicules, while some of the calcitic patches may have been desmas. Most of the spicules are connected to form a reticulate meshwork.

Types.—Holotype, C 108 (polished section), Department of Geology, University of British Columbia; Paratype, IT-312 (polished section), Department of Geology, University of Wyoming.

Horizon and locality.—Collected 294 feet above the base of the Gallatin formation (Upper Cambrian) (170 feet above the base of the upper limestone member as recognized by Miller, 1936) in the NE¼ NE¼ sec. 1, T. 29 N., R. 98 W., Beaver Creek Canyon, Fremont County, Wyoming.

MANUSCRIPT RECEIVED MAY 12, 1954

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EXPLANATION OF PLATE 49

FIGS. *1–3*—*Gallatinospongia conica* Okulitch and Bell, n. gen., n. sp. *1*, inner portion of the wall showing lacunae and felted spicules. Some spicules appear to be monaxons, ×36; *2*, isolated spicules located near the inner surface of the wall, ×36; *3*, inner portion of the wall showing felted spicules and calcitic patches, ×18. (p. 461)

JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 462–464, PL. 50, MAY 1955

THE CARBONIFEROUS GUIDE FOSSIL, *TYLONAUTILUS*, IN AMERICA

A. K. MILLER AND W. M. FURNISH
Iowa City, Iowa

ABSTRACT—A well preserved specimen is illustrated and described from the Upper Mississippian Fayetteville formation of northeastern Oklahoma. It is referable to *Tylonautilus nodosocarinatus* (Roemer) of the lower Namurian in the British Isles, Belgium, and Germany.

IN JUNE of 1954, J. Selwyn Turner of the University of Leeds wrote in regard to *Tylonautilus*, which in Europe has long served as an index to the *Eumorphoceras* zone of the lower Namurian, at the base of the Upper Carboniferous. He emphasized that this genus should be found in corresponding strata in the United States because on both sides of the Atlantic, faunas of this general age are remarkably similar. A few weeks later, Allen Graffham, then of the Tucker Tower Museum at Ardmore, Oklahoma, sent us a Fayetteville specimen which appears to be conspecific with those known from Great Britain and continental Europe. However, it does not constitute discovery of the genus in America, for as early as 1909 Girty described two immature representatives from the Caney shale of the Arbuckle region in southern Oklahoma. The affinities of his specimens had long been an enigma to us, but now it is clear that they correspond to the inner volutions of the Fayetteville form.

The specific relationships of the various European specimens that have been referred to *Tylonautilus* have been a moot question. In 1863 Roemer established the name *Nautilus nodoso-carinatus* for German specimens, whereas two years later Armstrong proposed *N. nodiferus* for a similar British individual. In 1891 Foord stated that the identity of the latter "with Römer's species is, however, beyond question." Nevertheless, in 1928 Pringle and Jackson disagreed with this "verdict," and their view has been accepted by Schmidt and Schwarzbach in Germany, Demanet in Belgium, and Trotter in England. However, in 1935 Wirth, while studying German material, came to the same conclusion as Foord. We have no specimens of *Tylonautilus* from Britain or continental Europe for comparisons, but our experience with Late Paleozoic nautiloids has convinced us that in comparable species there is a certain amount of variation. Therefore, we are inclined to believe that the differences between British and German individuals are of little taxonomic significance. Furthermore, we think that the American specimens had best be referred to the same species, though if one feels that they should be regarded as distinct, the name proposed by Girty is, of course, available.

It seems probable that the containing strata are of essentially the same age in the several regions from which this species is known. In Britain it is limited to the Pendleian and the Arnsbergian, where it is found in association with goniatites of the *Eumorphoceras* zone; and in Belgium and Germany it occurs with the same cephalopod assemblage, especially. *E. bisulcatum* Girty. The holotype of that species came from the very locality in Oklahoma that yielded the Caney specimens of *Tylonautilus* described by Girty. The Fayetteville formation, the source of the *Tylonautilus* we are studying, carries goniatites in Arkansas about 60 miles to the northeast, but they have never been illustrated and described in detail. As noted by Gordon (1953, p. 1427), both *Cravenoceras* and *Eumorphoceras* are represented in the middle Fayetteville, and they seem to indicate a correlation with the lower part of the *Eumorphoceras* zone in Britain. No goniatites were found in direct association with our *Tylonautilus*, and we do not know with certainty the relative stratigraphic position of the Fayetteville goniatites and this nautiloid. However, Professors George G. Huffman and Carl A. Moore of the University of Oklahoma have written us that at the locality where the *Tylonautilus* was

obtained, the Fayetteville is an easily recognized distinct lithologic unit. All in all, it therefore seems that the American representatives of *Tylonautilus*, like the British, are from the *Eumorphoceras* zone.

It is now known that in both Britain and America the stratigraphic ranges of *Eumorphoceras* and *Goniatites* overlap, though each of these genera can still be said to characterize zones in a general way. In this country, the latter occurs as low as the middle Meramecian of Indiana, and it is abundant in direct association with *Eumorphoceras* in the Barnett of Texas. Furthermore, this genus, *Goniatites*, is gradational with certain of the "gastrioceratids" of the Lower Pennsylvanian in Oklahoma, and extreme variants of these two forms are almost indistinguishable. The sequence of middle Carboniferous ammonoid zones established in Britain can not now be applied literally to American strata. For example, *Eumorphoceras bisulcatum*, which in Europe is limited to and characteristic of the Arnsbergian (E_2 zone), occurs in both the Barnett and the Caney formations together with *Goniatites*, *Lyrogoniatites*, *Neoglyphioceras*, and *Girtyoceras*, an assemblage of genera that in Europe is more or less characteristic of the underlying Bollandian (P_1 and P_2 zones). This fact, together with other considerations like the occurrence of "typical Keokuk brachiopods" in a coquina which Cloud and Barnes (1948, p. 56) regarded as lower Barnett, led to the conclusion that the formation, and therefore the *Eumorphoceras* zone in America, might be Meramecian (Miller and Youngquist, 1948, p. 662); whereas it now seems more logical to regard it as Chesterian. The above-mentioned coquina with Osagian brachiopods has recently been interpreted as distinct from the Barnett (Plummer, 1950, p. 28; Hass, 1953, pp. 70, 71). Notwithstanding, the recognition, here, of another index fossil of the European "E zone" is believed to be significant and confirms the correlation of the *Eumorphoceras bisulcatum* beds on opposite sides of the Atlantic.

TYLONAUTILUS NODOSOCARINATUS (Roemer)

Pl. 50, figs. 1–4

Nautilus nodoso-carinatus ROEMER, 1863, Deutsch. geol. Gesell., Zeitschr., Bd. 15, pp. 577–578, pl. 14, figs. 8a–8c; ROEMER, 1870, Geol. Oberschlesien, p. 84, pl. 8, figs. 19, 20.

Nautilus (*Discites*) *nodiferus* ARMSTRONG, 1865, Geol. Soc. Glasgow, Trans., vol. 2, pp. 74–75, pl. 1, figs. 6, 7; PEACH (in Geikie), 1900, Geol. Surv. Scotland, Mem., Fife and Kinross, pp. 236, 250.

Nautilus nodiferous YOUNG & ARMSTRONG, 1874, Geol. Soc. Glasgow, Trans., vol. 4, p. 280.

Nautilus nodiferus ARMSTRONG, YOUNG, & ROBERTSON, 1876, Cat. western Scottish fossils, pp. 59, 73, 80, 89, 91.

Pleuronautilus nodoso-carinatus FOORD, 1891, Cat. fossil Cephalopoda British Mus., Pt. 2, pp. 139–140; FOORD, 1891, Geol. Mag., n. ser., dec. 3, vol. 8, pp. 481–482; FOORD (in Hind et al.), 1901, British Assoc. Adv. Sci., p. 295; HIND, 1907, Naturalist, p. 94; BISAT, 1914, Yorkshire Geol. Soc., Proc., n. ser., vol. 19, table 3 (opp. p. 24); SMITH et al., 1925, Geologists Assn., Proc., vol. 36, p. 45; HEDLEY & WAITE, 1929, Univ. Durham Philos. Soc., Proc., vol. 8, pp. 149–150.

Coelonautilus gratiosus GIRTY, 1909, U. S. Geol. Surv., Bull. 377, pp. 9, 50, pl. 5, figs. 1-lb.

Tylonautilus nodiferus PRINGLE & JACKSON, 1928, Naturalist, pp. 373–378, pl. 11; WRIGHT, 1929, Naturalist, pp. 109–110; PRINGLE (in Eastwood et al.), 1931, Geol. Surv. England and Wales, Mem., Whitehaven and Workington, pp. 97, 99; PRINGLE (in Trotter and Hollingsworth), 1932, Geol. Surv. England and Wales, Mem., Brampton, p. 192; SCHMIDT, 1933, Preuss. geol. Landesanst., Jahrb., Bd. 54, p. 460; DEMANET, 1936, Mus. royal Hist. nat. Belg., Bull., t. 12, no. 44, pp. 1–10, pl. 1, figs. 1–4, pl. 2, figs. 1, 2; [part] JACKSON, 1946, Liverpool Geol. Soc., Proc., pt. 3, vol. 19, pp. 161–164, pl. 3; TROTTER, 1952, Liverpool and Manchester Geol. Jour., vol. 1, pp. 100, 102, 103; MOSLEY, 1954, Geol. Soc. London, Quart. Jour., vol. 109, p. 434.

Tylonautilus nodosocarinatus PRINGLE & JACKSON, 1928, Naturalist, p. 374; SCHMIDT, 1933, Preuss. Geol. Landesanst., Jahrb., Bd. 54, p. 460; WIRTH, 1935, Neues Jahrb., Beil.-Bd. 73, Abt. B, pp. 247–249, pl. 11, fig. 14; SCHWARZBACH, 1937, Neues Jahrb., Beil.-Bd. 78, Abt. B, p. 449, pl. 20, fig. 39.

(?)*Tylonautilus nodiferus* early mutation STUBBLEFIELD (in Hartley), 1945, Irish Nat. Jour., vol. 8, p. 259; [part] JACKSON, 1946, Liverpool Geol. Soc., Proc., pt. 3, vol. 19, pp. 162–163; TROTTER, 1952, Liverpool and Manchester Geol. Jour., vol. 1, pp. 86, 87; STUBBLEFIELD, 1953, Geol. Surv. Great Britain (England and Wales), Mem., Bradford & Skipton, pp. 92–93.

The specimen under consideration is moderately well preserved in dark dense limestone, and all but the extreme adoral part of it is septate. It is about 50 mm. in diameter. At the adoral end of the phragmocone the conch is some 18 mm. high and 29 mm. wide, and the ventral sulcus is 2 mm.

deep. The dorsal impressed zone is very shallow. The adapical portion of the specimen consists of crystalline calcite, but clearly the phragmocone was a little more than two volutions in length and enclosed an umbilical perforation.

On each of the lateral zones of the conch, there are large transverse ribs and six pairs of prominent longitudinal lirae which form nodes as they cross the ribs. A preserved portion of the test shows that these features are much more conspicuous on the surface of the shell than on the internal mold. Ribs and lirae are not present on the ventral sulcus or the umbilical walls.

Each suture forms a ventral lobe, which merely reflects the shape of the cross section. The siphuncle is located distinctly closer to the venter than the dorsum.

Remarks.—Although this individual is considerably larger than those described from the Caney formation, its maximum diameter is somewhat less than half that attained by conspecific European representatives. In the latter, the surface markings of the test are more conspicuous, but this difference is believed to be due largely to preservation and relative size, because the surface markings of our Fayetteville specimen increase in prominence adorally. It may well be that a direct comparison of the various specimens now referred to this genus will show that there are differences which are sufficiently constant to justify the recognition of distinct species. Late in 1954, Stubblefield wrote us that a form which in 1945 he had regarded as an "early mutation" of *T. nodiferus* should "properly be termed a new species. It differs . . . in that nodes are absent from the two innermost pairs of ventral lirae." Accordingly, in our synonymy the references to this form are questioned. Acknowledgment is also due to J. Selwyn Turner for reading our manuscript and making constructive suggestions.

Insofar as we are aware, the only form closely similar to this species is *Tylodiscoceras unicum* Miller and Collinson of the Meramecian in south-central Kentucky. In cross section, but not sculpture, these two are comparable.

Mr. Francis Hemming has advised us that the Code of the International Rules of Zoological Nomenclature, as prescribed by the Paris (1948) Congress, is now being drafted. This forthcoming edition provides that the hyphen be omitted in specific names like that of the form under consideration.

Occurrence.—Fossiliferous limestone bed some 20 feet below top of Fayetteville formation on east side of new portion of Oklahoma State Highway 10 at Braggs Mountain, near Braggs, Muskogee County, Oklahoma. The two fragments Girty described in 1909 came from the Caney formation south of Wapanuca, Johnson County, Oklahoma. Congeneric specimens are of widespread occurrence in strata of about the same age in England, Wales, Scotland, Northern Ireland, Belgium, and Germany.

Figured specimen.—State University of Iowa, 9819.

MANUSCRIPT RECEIVED DECEMBER 21, 1954

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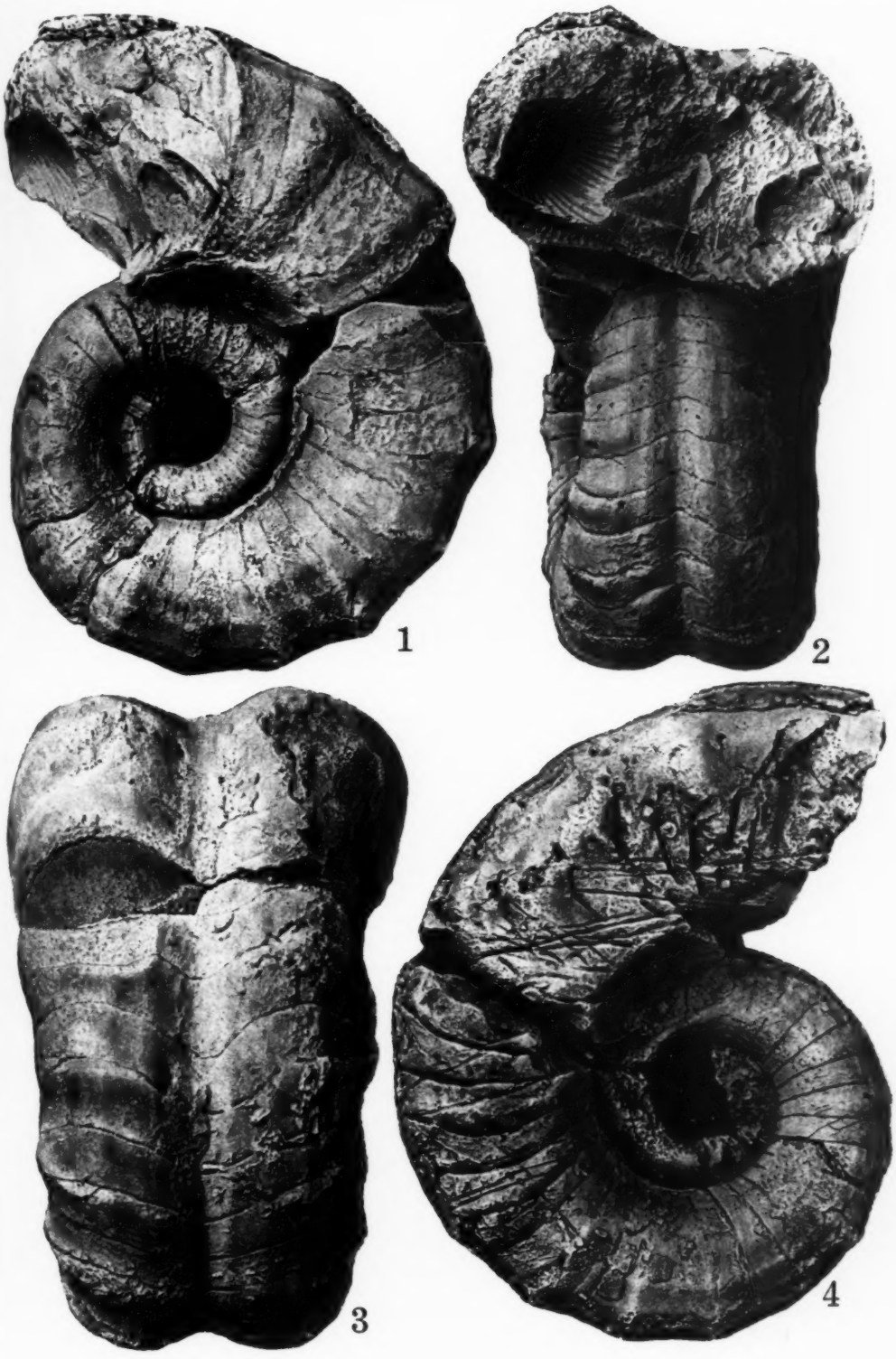
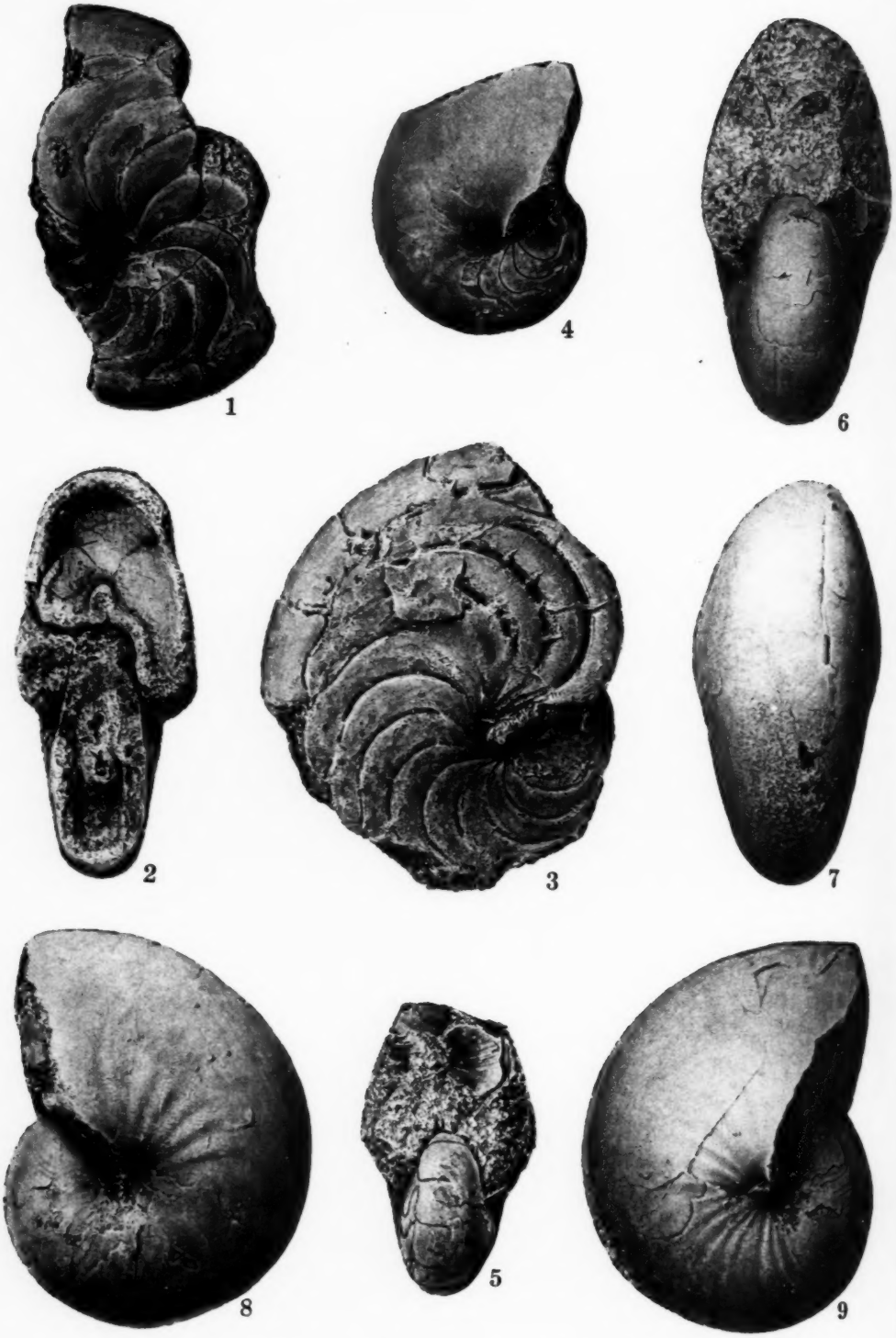
EXPLANATION OF PLATE 50

FIGS. *1–4*—*Tylonautilus nodosocarinatus* (Roemer). Four views of a specimen from the Fayetteville formation at Braggs Mountain in northeastern Oklahoma, ×2. (p. 463)



Miller and Furnish, Mississippian *Tylonautilus* in America



Miller, Furnish and Paguaga, Aturias from Costa Rica
Miller and Furnish, Aturias from Chile

JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 465–466, PL. 51 (FIGS. 1–3), MAY 1955

ATURIAS FROM COSTA RICA

A. K. MILLER, W. M. FURNISH, AND ALFONSO SEGURA PAGUAGA
Iowa City, Iowa, and Guadalupe, Costa Rica

ABSTRACT—Two representatives of *Aturia peruviana* Olsson are described from the Eocene? about 45 miles west of Limón. These are the first fossil cephalopods to be recorded from Costa Rica.

A FEW years ago two aturias were found in central Costa Rica. Though small, they are rather well preserved and merit careful consideration for they are the first nautiloids to be reported from the country. Both are completely septate internal molds preserved in light gray calcareous sandstone. Their general nature is elucidated by the accompanying illustrations (Pl. 51, figs. 1–3), but it should perhaps be stated that the maximum dimension of the larger individual is about 65 mm., that of the smaller, 40 mm. These specimens have been somewhat distorted during preservation, so measurements more nearly accurate than those which can be obtained from our photographs would have little significance.

These two individuals appear to be conspecific, and they are referable to *Aturia*. Representatives of that genus are known from many widely separated localities in various parts of the world. They range from the base of the Eocene well up into the Miocene, and some may possibly have been found in slightly older strata. On the Atlantic-Gulf Coastal Plain of North America, aturias are much more common in the Eocene than in the later Tertiary, but this generalization does not seem to hold for the rest of the world.

Because of their small size, the two specimens under consideration are assumed to represent only immature portions of the conch. Large aturias attained diameters of more than 500 mm., including the body chamber. All representatives of the genus *Aturia* are so much alike that we can not ascertain from these two Costa Rican individuals alone whether they came from Eocene, Oligocene, or Miocene beds. According to Branson and Sapper, strata of all three of these ages are present in the region where our specimens were collected. In addition to these cephalopods, Segura Paguaga secured many fossils there, including large foraminifers, corals, brachiopods, echinoids, ostreids, turritellids, crustaceans, and shark teeth. These have not yet been studied in detail, but we expect that in the future they will yield a more nearly precise age determination than the aturias. Comparable cephalopods are known to have a wide distribution in the Eocene of tropical America, where the most abundant species is *Aturia peruviana* Olsson. The larger of the specimens we are studying is strikingly similar to certain of those Miller (1947, pl. 79, figs. 1, 2; pl. 81, figs, 1, 2) illustrated from the Eocene of Peru and Panama, and there seems to be good reason to consider them as conspecific.

It should be stated that some time ago Sr. Segura Paguaga prepared an unpublished

EXPLANATION OF PLATE 51

Aturias from Costa Rica

FIGS. 1–3—*Aturia peruviana* Olsson. Two specimens from the Eocene? in the Quebrada del Patincho, Finca Montealegre, southeast of the Río Reventazón, near Peralta, some 45 miles west of Limón, Costa Rica; ×1½ (*1, 2*) and ×13. (p. 465)

Aturias from Southern Chile

4–9—*Aturia brueggeni* Ihering. Two views of one specimen and four of another, both from the Eocene of Cerro de la Oveja, south of Puerto Natales, Magallanes, Chile; all ×2. (p. 467)

account of the aturias on which this paper is based. The larger specimen is to be deposited in his private collection, whereas he has donated the smaller one to the State University of Iowa (catalogue number, 9818). Acknowledgment is also due to Dr. F. G. Engelberts of San Jose for facilitating arrangements in Costa Rica, to Mr. Frederick Leach of Iowa City for retouching the photographs on the accompanying plate, and to the Graduate College of the State University of Iowa for making the completion of the report financially possible.

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JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 467–468, PL. 51 (FIGS. 4–9), MAY 1955

ATURIAS FROM SOUTHERN CHILE

A. K. MILLER AND W. M. FURNISH
Iowa City, Iowa

ABSTRACT—Three small specimens from the Eocene near Puerto Natales are considered. They appear to be referable to *Aturia brueggeni* Ihering, originally described from nearby Tierra del Fuego.

IN 1953 Dr. Giovanni Cecioni F. of Punta Arenas on the Strait of Magellan sent us for study three small aturias, which are exceptionally well preserved. They came from Cerro de la Oveja, between the Río Rubens and Lago Anibal Pinto, south of Puerto Natales, Depto. Ultima Esperanza, Magallanes, Chile. These specimens are all very similar morphologically and lithologically, and they are composed of compact dark gray arenaceous limestone. Although they retain considerable portions of the test and thereby elucidate the surface markings of the conch, they also reveal the shape of the sutures.

In size, these three individuals are all of the same order of magnitude, and, peculiarly, two of them retain essentially all of the body chamber. The maximum dimension of the largest is about 30 mm.; that of the other complete specimen is almost 25 mm.; and the third, which is septate throughout, attains a diameter of a little less than 15 mm. The two type specimens of *A. brueggeni* Ihering, from the Boquerón beds on the opposite side of the Strait of Magellan on Tierra del Fuego, are also of far less than average dimensions, having diameters of only 25 and 30 mm., but at least the smaller one is completely septate. According to Feruglio (1949, t. 2, pp. 164–165) several other congeneric forms are known from this far south (some 50–55° latitude), but no information is available as to their size.

Because all five of the aturias described from this southernmost region are of approximately the same diameter, it may be logical to assume that they represent a species in which the conch attained only modest proportions, less than 50 mm. This idea is substantiated by the fact that the apertural margins of our essentially complete specimens are slightly but distinctly flared, indicating maturity. Elsewhere in the world, congeneric forms commonly had a diameter of 250 mm., and in rare cases as much as 500 mm. However, the small size of *A. brueggeni* may not be directly related to an extreme of latitude, for average-sized specimens are known from only 400 miles to the north in both Chile and Argentina. In the northern hemisphere, aturias have been found in Alaska at some 60° latitude, where they are known to have reached a diameter of well over 150 mm. Several factors may therefore have contributed to the size attained by different species of *Aturia* beside the effects of high latitude.

The test appears to be very thin. The growth lines are quite distinct, and they form prominent broadly rounded lateral salients and a more narrowly rounded ventral sinus. On the body chamber of the illustrated specimens there is a series of small rounded ribs parallel to the growth lines. They are relatively prominent in the umbilical regions and become indistinct ventrally. The umbilicus is closed.

The body chamber is rarely preserved in aturias because it bears no internal supports and the test is thin. However, in a large specimen from the Eocene of Panama, some 300 mm. in diameter, the length of the body chamber was observed to be half a volution, as in modern *Nautilus*. Our two complete specimens retain considerable portions of the apertural margins, which are flared in the umbilical regions, and in both of them the body chamber is half a volution long.

As shown by figures 4 and 5 on the accompanying plate, the sutures are typical of advanced representatives of the genus *Aturia*. The number of camerae per volution is about average, and the sutures contact one another in the adoral portion of the phragmocone. Most other species at com-

paral le dimensions have somewhat more primitive sutures.

The preservation of these figured specimens is such that they could be prepared to show details of the early ontogenetic development of the conch. However, because of the remoteness of the locality from which they come, we are reluctant to sacrifice them. It is hoped that the same locality will yield material for such preparation.

The three specimens on which this report is based are in the collections of the Empresa Nacional del Petroleo, Magallanes, where they bear the number G1337. The officials of that company generously loaned us the fossils for study, Mr. Frederick Leach retouched the photographs, and financial assistance was provided by the Graduate College of the State University of Iowa.

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JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 469–474, PLS. 52–54, MAY 1955

NEW GENERA OF PERMIAN BRACHIOPODS FROM WEST TEXAS[1]

G. ARTHUR COOPER AND FRANCIS G. STEHLI
U. S. National Museum and California Institute of Technology[2]

ABSTRACT—Three new genera and three new species of brachiopods from West Texas are described: *Coscinophora*, genotype, *C. nodosa; Ctenalosia*, genotype, *C. fixata;* and *Spyridiophora*, genotype, *S. distincta. Marginifera reticulata* King, 1930, is referred to *Spyridiophora*. Specimens of each of these exhibit unusual morphological features revealed when they were dissolved from Permian limestones of the Sierra Diablo and Glass Mountains Permian areas.

THE species described below are based on unusual specimens derived from solution in acid of Permian limestone from West Texas. Some of the specimens were derived from residues obtained at the American Museum of Natural History from the Diablo Plateau region north of Van Horn, Texas. Other specimens from the Glass Mountains of West Texas were obtained from residues prepared at the U. S. National Museum. In comparing notes on the various residues it was discovered that a few peculiar genera were common to both regions of Texas. It was, therefore, decided to pool our material and jointly describe these unusual specimens.

Each of the new genera reveals features hitherto unknown among their kind. *Coscinophora* belongs to the family Oldhaminidae but it has a myophragm in the pedicle valve and the lateral lobes are broken into rows of beads. In accord with this the lobes of the brachial valve are partially cemented except where they fit over the beads. At these points a hole remains; consequently, the brachial valve looks to be a veritable sieve. *Ctenalosia* is one of the Strophalosiidae which has developed teeth and sockets in a row on the posterior margins, a row of teeth in the pedicle valve and a row of sockets in the brachial valve. *Spyridiophora* is a beautifully sculptured productid, unique because of the elevation and fusion of the adductor platforms to form a small "basket" inside the brachial valve. These new interior features are of interest in morphology and the evolution of these peculiar brachiopods.

[1] Publication of the Division of Geological Sciences, California Institute of Technology, Pasadena, California. Contribution No. 706.

[2] Published by permission of the Secretary of the Smithsonian Institution.

SYSTEMATIC PALEONTOLOGY

Genus COSCINOPHORA Cooper & Stehli, n. gen.

(Gr. coscinum—sieve; phoros—to bear)

Genotype.—Coscinophora nodosa Cooper & Stehli, n. sp.

Diagnosis.—Large, attached, massive-shelled Oldhaminidae. Pedicle interior with prominent muscle scars divided by a myophragm; median and lateral ridges broken into series of discrete beads. Brachial valve secondarily massive posteriorly; anteriorly pinnate with the lobes regularly united by dissepiments producing a pattern of holes.

Discussion.—Coscinophora is easily distinguished from other Oldhaminidae of similar size if any part of the interior of the pedicle valve is visible, for the beaded appearance of the median and lateral ridges is distinctive.

In his study of the brachiopods of the Glass Mountains R. E. King (1930) described a species belonging to this genus as *Lyttonia hortoni* King. Unfortunately specimens of this form are rare, and the material upon which its diagnosis was based, very poor. King's specimens show only the generic character of beaded ridges; they do not show the more subtle features upon which genera and species are based. For this reason we have been unable to identify our excellent material with *L. hortoni*. We therefore propose to restrict the name *Lyttonia hortoni* to King's holotype, and propose the name *Coscinophora nodosa*, n. gen., n. sp., for the species which we describe below.

Coscinophora is known only from the Glass

Mountains where it occurs in the Wolfcamp, Leonard and Word formations. It is common in a few places where these shells lived in small banks like oysters. Evidently the conditions under which *Coscinophora* existed differed sharply from those of other Oldhaminidae of similar form, for the two types have not been found together. The species is commonly associated with sheet-like bryozoan colonies which often grow over the valves.

COSCINOPHORA NODOSA Cooper & Stehli, n. sp.
Pl. 52, B, figs. 17–20

Diagnosis.—Medium to very large sized *Coscinophora*, a large specimen about equal in size to one's hand. Pedicle valve cemented by much of the exterior surface and of highly irregular shape; valve generally modately convex but sometimes almost saucer-like; posterior margin generally recurved anteriorly to form a short hood; lateral margins sometimes recurved dorsally. Pedicle interior with the median and lateral ridges broken into many discrete units which produce a beaded or toothed appearance. A well developed articulation area bearing numerous striations is present posteriorly for the reception of the brachial valve. In front of the hinge a depressed area contains well developed muscle scars; the large dendritic adductor scars are medially placed one on either side of a thin, high myophragm. At either side of the adductors are narrow elongate non-dendritic diductor scars bounded laterally by low myophragms or ridges separating the depressed muscle area from the level of the remainder of the valve.

Brachial valve very massive and fused into a solid plate by secondary deposits for about one-third its length. Anteriorly it assumes the pinnate form characteristic of the family, except that numerous narrow dissepiments unite the lobes rather regularly at intervals of 1–2 mm. producing a reticulate pattern of holes. In closure of the valves the beads of the ridges in the pedicle valve close this network of holes in the brachial valve. Surface of the valve papillose. Brachial interior with a reduced but clearly functional cardinal process. Anterior to the hinge at either side of the median slit, elongate narrow adductor scars appear to be present but are slightly impressed.

Measurements.—Specimens too incomplete anteriorly to give an accurate measure of length and width.

Types.—Holotype USNM 124121b; figured paratype 124121a.

Horizon and locality.—Permian (Leonard formation—*Institella* zone), just east of Split Tank, Hess Canyon Quadrangle, Texas.

Discussion.—No species of this genus other than *C. hortoni* King has been described previously. King's specimen is too imperfect for comparison with *C. nodosa*.

Genus CTENALOSIA Cooper & Stehli, n. gen.
(Gr. ktenos—comb)

Genotype.—*Ctenalosia fixata* Cooper & Stehli, n. sp.

Diagnosis.—Small Strophalosiidae attached to a foreign object by cementation of the pedicle umbo and by root-like spines; irregular in shape; ears obsolete. Pedicle valve with the anterior slope smooth or obscurely costate and bearing few spines other than those used in attachment; valve deep but of irregular shape because of its attached habit; interarea well developed; delthyrium closed by a thin pseudodeltidium. Brachial valve operculiform; ornamented with irregular concentric wrinkles and pits; without spines.

Pedicle interior with the hinge bearing numerous sharp, conical teeth; adductor muscles inserted on a low platform and divided by a thick, low myophragm; diductor scars lightly impressed. Brachial interior with the hinge bearing numerous sockets; cardinal process variable, irregularly inclined, generally trilobed, shaft splitting into two parts at the base; adductor muscle scars at base of process on platforms, depressed posteriorly while raised anteriorly; median septum low and short, located in front of the adductor platforms; brachial ridges strongly impressed; anterior margin of valve flattened and thickened but with a channel entering the valve between the brachial ridges.

Discussion.—This genus resembles in many characters the more typical Strophalosiidae. It is unique, insofar as we are aware, in the possession of abundant hinge teeth and sockets. If the Productacea arose from the stropheodonts, as seems probable, then the presence of teeth in *Ctenalosia* presents

an interesting case of the loss of a structure and its later reappearance. It must be noted that the teeth are different in the two groups. In the strophеodonts the dentition consists of interlocking ridges and depressions in each valve. In *Ctenalosia* on the other hand the teeth are distinctly limited to the pedicle valve and the sockets to the brachial valve.

The exact adaptive significance of the teeth and sockets, especially in so small a form, is obscure, but their reappearance indicates a critical need for rigid articulation.

Representatives of the genus have been found in limestone No. 2 of the Word formation in the Glass Mountains and in the lower Getaway limestone of the Guadalupe Mountains. In both cases the rock sampled represented an accumulation of organic hard parts to which *Ctenalosia* is attached.

The peculiar plicate anterior margin of the brachial valve in this species served to guide water currents. Whether incurrent or excurrent streams passed through this median aperture can not now be determined as nothing is certainly known of the lophophore of the Productacea. *Ctenalosia fixata* might be confused with some contemporary species generally referred to *Heteralosia* but is easily distinguished by the absence of spines along the anterior slope of the pedicle valve and by the hinge teeth. It might also be confused with *Productus? pileolus* Girty but differs in the presence of costation and absence of concentric ornamentation on the pedicle valve and ear spines. Striking internal differences also separate the two species, *P.? pileolus* having the anatomy of the aulostegids.

CTENALOSIA FIXATA Cooper & Stehli, n. sp.
Pl. 52, A, figs. 1–16

Diagnosis.—*Ctenalosia* in which root-like attachment spines are limited to the margins of the cemented pedicle beak while the free anterior slope bears few or no spines. Anterior slope finely but obscurely costate or apparently smooth in some individuals, costae increasing by bifurcation. Pedicle interarea well developed in uncrowded specimens. Brachial valve with the visceral disc flat to moderately concave, margins often geniculate and frequently bearing a lamellar fringe of outgrown and broken trails; valve characteristically with concentrically arranged wrinkles and pits, but sometimes nearly smooth.

Pedicle interior with four to six sharp conical teeth along the hinge, on each side of the cardinal process the teeth increasing in size away from the median line. Brachial interior with four to six deep sockets on either side.

Discussion.—This is the only known species of *Ctenalosia*. Where it occurs it is often common but except in good silicified material it might well pass unnoticed because of its small size and attached habit.

Measurements in mm.—Holotype: length 7.0, width 8.1, thickness 3.5, hinge width 4.7.

Types.—Holotype USNM 124123a; figured paratypes USNM 124123b–i, 124161a; unfigured paratypes USNM 124123j, 124161b.

Horizon and locality.—Permian (Word formation, limestone No. 2), west slope and crest of low hill, 3.7 miles N. 36° E. of the Hess Ranch, Hess Canyon (15 minute) Quadrangle, Texas.

Permian (Cherry Canyon formation, Getaway limestone member), south of U. S. highway 62, 2.5 miles S. 8° W. of Pine Spring Camp, U.S.G.S. Oil and Gas Investigation Preliminary Map 18, Guadalupe Mountains, Texas.

Genus SPYRIDIOPHORA Cooper & Stehli, n. gen.
(Gr. spyridium—a little basket)

Genotype.—*Spyridiophora distincta* Cooper & Stehli, n. sp.

Diagnosis.—Small, an inch or slightly more in width, transverse unattached Productacea. Pedicle valve with a median sulcus, moderately geniculate, posterior slope with a reticulate pattern of tubercles formed by intersecting costae and concentric folds; anterior slope ornamented with high rounded costae which occasionally bear spines; intercostal grooves deep and narrow; ears separated from the visceral area by a spine bearing ridge or by a row of spines in the position of the ridge; a single row of spines running from the beak onto the ears and diverging gradually from the hinge; ears bearing a tuft of enlarged spines. Brachial valve sharply geniculate with the visceral

disc reticulate and the trail costate only; spines absent.

Pedicle interior with sharp ridges separating the ears from the visceral disc. Brachial interior with the visceral disc surrounded by a ridge which originates at the cardinal process and is high postero-laterally and reduced or absent anteriorly; cardinal process bilobed, short, anteriorly united with the adductor muscle platform which is raised high above the valve floor; muscle platforms consisting of two subparallel or partly fused essentially vertical plates bearing discrete platforms or platforms fused to form a spyridium[1] with a subjacent cella; median septum short and high to absent; brachial ridges poorly impressed and directed anteriorly at 45 degrees.

Discussion.—*Spyridiophora* has a distinctive external appearance due to the very strong reticulation of the umbo of the pedicle valve. Its most remarkable character is, however, the elevation of the brachial adductor muscles on high platforms. This feature immediately distinguishes it from other genera of the Productacea. Representatives of *Spyridiophora* occur in the Glass Mountains, the Sierra Diablo, perhaps China and the Carnic Alps.

[1] The term *spyridium* is here introduced for this peculiar muscle bearing "basket," for no existing term seems appropriate. *Spondylium* is used for a spoon-like structure in the pedicle valve formed by the union of the dental plates and so clearly can not be applied. *Cruralium* is applied to a spoon-like structure in the brachial valve arising as an outgrowth from the hinge area and supported by a median septum. A *spyridium* in contrast is formed, in this case, in the brachial valve, by the union of adductor muscle platforms elevated high above the valve floor by special vertical plates without the involvement of the median septum.

SPYRIDIOPHORA RETICULATA (King)

Pl. 53, A, figs. 1–8; Pl. 53, B, figs. 9–18

Marginifera reticulata KING 1930, p. 89, pl. 22, figs. 3–10.

Diagnosis.—*Spyridiophora* in which a pronounced, narrow median sulcus in the pedicle valve extends nearly to the beak. Hinge line probably extended by elongate ears bearing enlarged spines, but none of our specimens show complete ears; ridge above the ears seldom well developed but its position marked by a row of spines from the

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EXPLANATION OF PLATE 52

A. *Ctenalosia fixata* Cooper and Stehli, n. gen., n. sp. (p. 471)

FIGS. *1–14—1–5*, Respectively brachial, pedicle, side, posterior and anterior views of a complete individual, ×3, holotype USNM 124123a; showing apical cicatrix and thick anchor spines; *6*, brachial view of a coarsely silicified specimen, ×3, showing interarea and interlocking teeth along the hinge-line, paratype USNM 124123b; *7*, posterior of another paratype, ×3, showing the elongate interarea and nearly flat pseudodeltidium, USNM 124123c; *8*, *9*, anterior and interior views of a large pedicle valve showing costellate, non-spinose anterior slope, anchor spines, adductor callosities and median ridge, ×3, paratype USNM 124123d; *10*, interior view of a small pedicle valve showing attachment to another productid spine, ×3, paratype USNM 124123e; *11–14*, interior views of four brachial valves showing teeth along posterior margin, median septum, adductor callosities and brachial ridges, ×3, paratypes respectively 124123f, g, h, i.

Permian (Word limestone No. 2), southwest slope and crest of low hill, 3.7 miles N. 36° E. of the Hess Ranch, Hess Canyon (15 minute) Quadrangle, Texas.

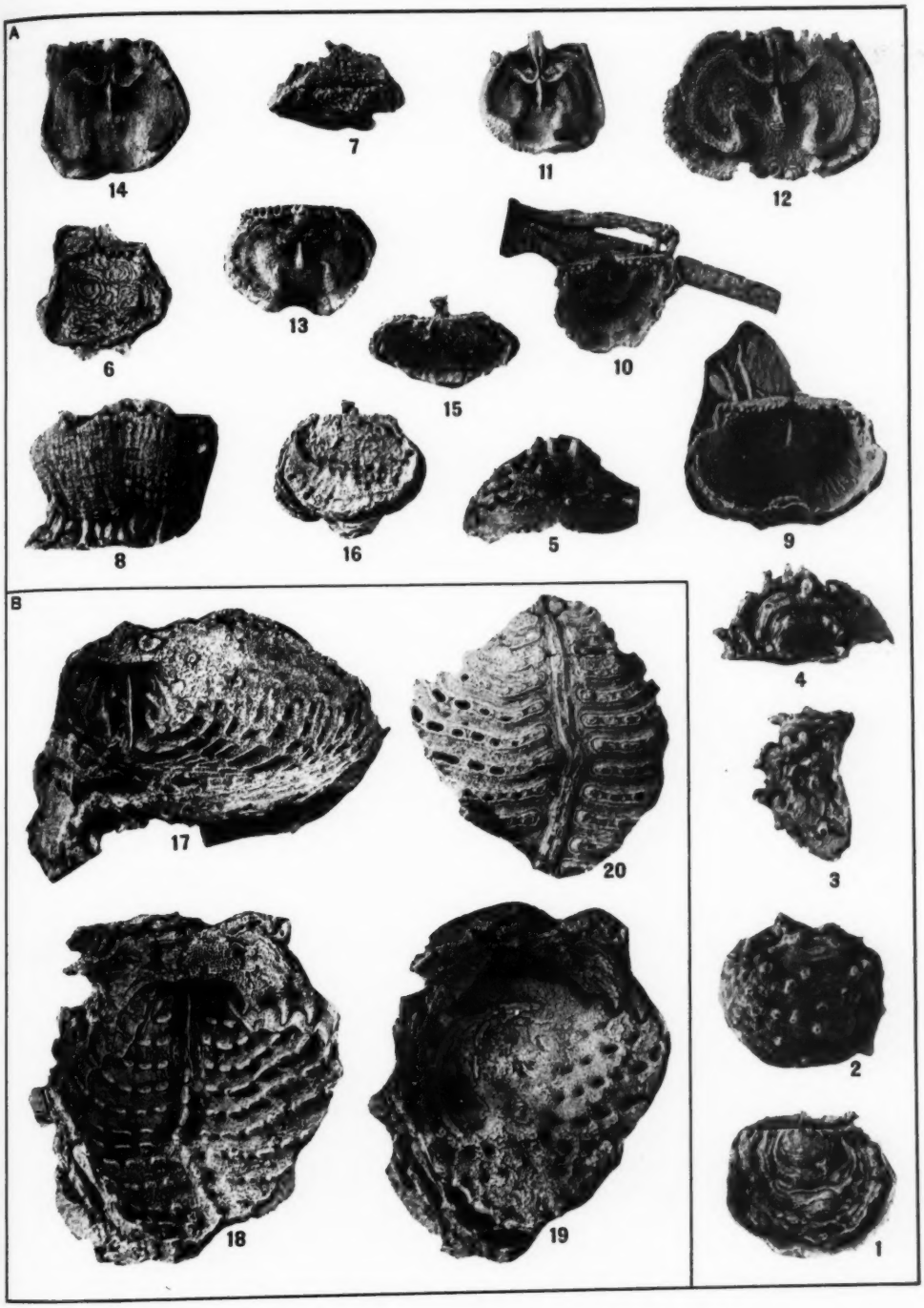
15, *16*, Posterior and brachial views of a brachial valve showing the lobate cardinal process, ×3, paratype USNM 124161a.

Permian (Cherry Canyon formation—Getaway member), south of U. S. highway 62, 2.5 miles (S. 8° W. of Pine Spring Camp, U.S.G.S. Oil and Gas Investigation Preliminary Map 18, Guadalupe Mountains, Texas.

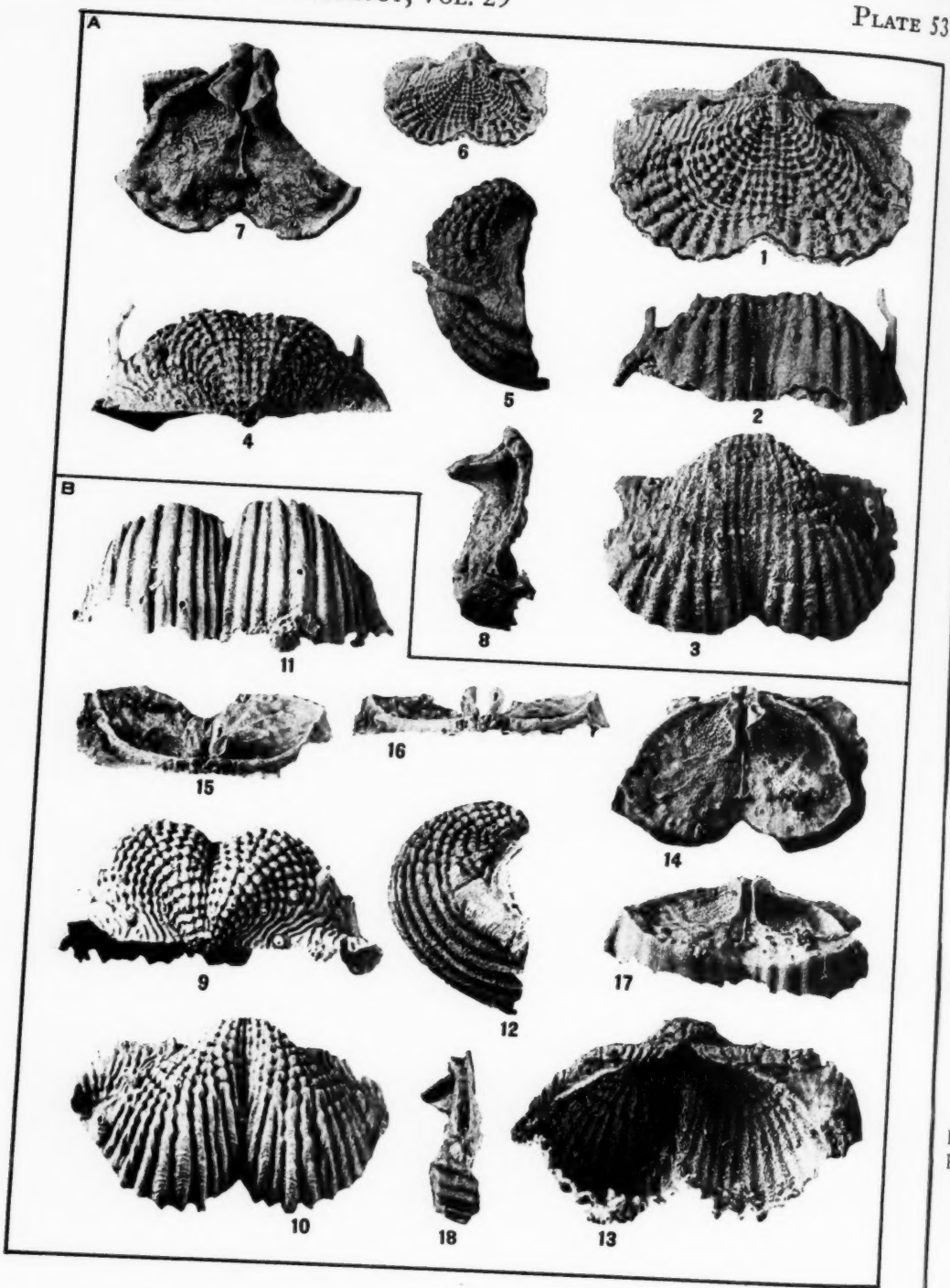
B. *Coscinophora nodosa* Cooper and Stehli, n. gen., n. sp. (p. 470)

FIGS. *17–20—17*, Interior of a pedicle valve showing beaded lateral and median ridges, thin, elevated myophragm and hood, ×1, paratype USNM 124121a; *18*, interior of another pedicle valve showing myophragm separating dendritic adductor scars and strong hood, ×1, holotype USNM 124121b; *19*, the holotype with the brachial valve in place showing the sieve-like character, the dissepiments connecting the lobes and the massive posterior, ×1; *20*, interior of the brachial valve of the holotype showing sieve-like character and lateral lobes, ×1. Note reduced but functional cardinal process.

Permian (Leonard formation—*Institella* zone), just east of Split Tank, Hess Canyon Quadrangle, Texas.



Cooper and Stehli, Permian brachiopods, West Texas



Cooper and Stehli, Permian brachiopods, West Texas

beak to near the anterior margin. Posterior slope with coarse tubercles in reticulate pattern; tubercles occasionally giving rise to short spines; costae arising in the reticulate area and increasing there by bifurcation to attain their maximum number at or slightly anterior to the edge of the reticulate area. Anterior slope with high, rounded costae bearing occasional spines and separated by deep, narrow intercostal grooves; a few of the medial costae generally converge in the sulcus. Brachial valve with the flat visceral area medially interrupted by a low fold and bearing a coarse reticulate ornamentation which becomes reduced toward the umbo; trail costate only.

Pedicle interior with a prominent ridge indicating the position of the sulcus; muscle scars poorly impressed.

Measurements in mm.—Hypotype USNM 124118a; length 14.0, width 25.6+, thickness?, surface length 25.0, half-measure of hinge-width 11.0=22.0+.

Types.—Lectotype: Yale Peabody Museum 11724; figured hypotypes AMNH 27932:1, :2, USNM 124118a, b.

Horizon and locality.—Permian (base of Bone Spring formation), Figure 2 Ranch, Sierra Diablo, about 32 miles north of Van Horn, Culberson County, Texas.

Permian (top Wolfcamp formation), knob on west side of entrance to Sullivan Ranch Canyon, 3.5 miles N. 7° E. of Decie Ranch House, Altuda (15 minute) Quadrangle; upper Leonard (fossil bed in eastern Hess facies), 3.9 miles N. 67° E. of Hess Ranch, Hess Canyon (15 minute) Quadrangle, Texas; lectotype from Leonard formation on south side hill 0.6 miles north of hill 5021, Altuda (15 minute) Quadrangle, Texas.

Discussion.—King's (1930) three cotypes have been studied and though his specimens are extremely poor they show sufficient detail to indicate that our specimens from near the Wolfcampian-Leonardian boundary on the Decie Ranch in the Glass Mountains and from the lower part of the Bone Spring formation in the Sierra Diablo are conspecific. In order to fix King's species we select his brachial valve YPM 11724 as lectotype. King believed that his species was closely related to *Marginifera whitei* but in this he was incorrect for the two species must be referred to different genera. Examination of King's cotypes of *Marginifera reticulata angusta* shows them to be so poorly preserved as to be beyond confident identification; but they almost certainly are not congeneric with *Marginifera reticulata.*

Spyridiophora distincta Cooper & Stehli, n. sp.
Pl. 54, figs. 1–17

Diagnosis.—*Spyridiophora* in which the pedicle valve bears a fairly broad shallow sulcus generally arising some distance an-

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Explanation of Plate 53

A. *Spyridiophora reticulata* (King) (p. 472)

Figs. *1–8—1–5*, Respectively brachial, anterior, pedicle, posterior and side views of a nearly complete hypotype, ×2, showing strong reticulation and thick spines, AMNH 27932:1; *6*, the same hypotype, ×1; *7*, *8*, interior and side views of the brachial valve showing spyridium grown to cardinal process and indistinct but elevated brachial ridges, ×2, hypotype AMNH 27932:2.

Permian (base of Bone Spring formation), Figure 2 Ranch, Sierra Diablo, about 32 miles north of Van Horn, Culberson County, Texas.

B. *Spyridiophora reticulata* (King) (p. 472)

Figs. *9–18—9–12*, Respectively posterior, pedicle, anterior and side views of a complete specimen, showing deep sulcus of pedicle valve, strongly reticulated visceral region and costate trail, ×2, hypotype USNM 124118a; *13*, interior of the preceding specimen showing lateral oblique ridges crossing the ears and the median elevation formed by the deep exterior sulcus, ×2; *14*, interior of the brachial valve showing spyridium, ×2, hypotype USNM 124118b; *15*, *16*, posterior view of the preceding specimen tilted and in profile showing spyridium, and subperipheral rim, ×2; *17*, anterior view of preceding showing plates supporting spyridium and bounding the cella, ×3; *18*, side view of preceding showing spyridium in profile, ×2.

Permian (top of Wolfcamp formation), knob on west side of entrance to Sullivan Ranch Canyon, 3.5 miles N. 7° E. of Decie Ranch House, Altuda (15 minute) Quadrangle, Texas.

terior to the beak. Hinge line extended by elongate ears, a row of enlarged spines running laterally from the beak onto the ears and diverging slightly from the hinge; posterolateral to this row the ears bear a tuft of large spines, Spine-bearing ridge pronounced, separating the ears from the visceral area. Anterior slope marked by a fine reticulate ornament. Trail with high rounded, spine-bearing costae running to the front; costae not conspicuously bifurcating in the reticulate area, separated by deep narrow intercostal grooves; costae showing little tendency to converge into the sulcus. Brachial valve with the visceral disc finely reticulate; trail costate only.

Pedicle interior without a conspicuously raised median ridge, but with a raised area for muscle insertion in the umbo. Interior ornamented with rows of fine papillae following the positions of the external costae. Brachial interior with the adductor platforms fused to form a spyridium while the supporting plates diverge toward the floor to form a small triangular cella. Median septum short but usually conspicuous.

Measurements in mm.—Holotype: length 26.0, surface length 31.0, half-measure hinge-width 17.4=34.8, thickness 10.1; paratype USNM 124116b: length 16.4, surface length 32.0, half-measure hinge-width 20.4=40.8, thickness 11.0.

Types.—Holotype USNM 124117; figured paratype USNM 124116a, b, e; unfigured paratypes USNM 124116c, d.

Horizon and locality.—Permian (Wolfcamp formation, bed 9), at 4700 feet elevation on west side of hill 0.97 mile S. 82° W. of hill with elevation 5060 feet, Wolfcamp Hills, Hess Canyon (15 minute) Quadrangle, Texas.

Discussion.—This species is the one to which King (1930) applied the name *Productus gratiosus occidentalis* Schellwien. King erroneously made his identification of this form from plates published by Chao (1928) rather than from the original figure of Schellwien which he regarded as too poor for detailed comparison. Chao seems in his turn to have had some reservations about the identity of his material with that of Schellwien, pointing out several differences which he regarded as minor. Thus the identification is untenable.

Spyridiophora distincta differs from *S. reticulata* King in the wider shell, less deeply sulcate pedicle valve, shorter sulcus in pedicle valve, and finer reticulation.

MANUSCRIPT RECEIVED NOVEMBER 3, 1954

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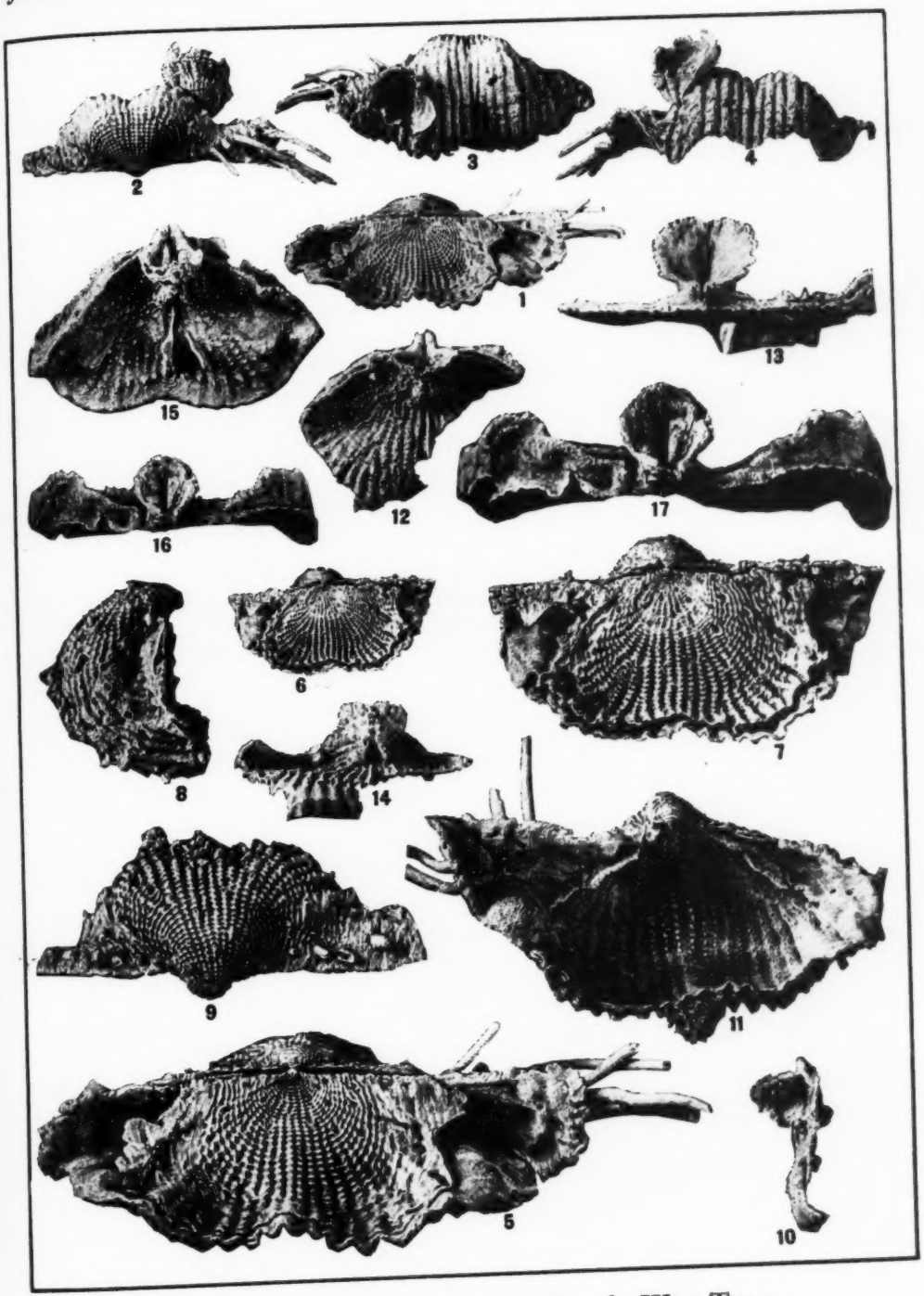
EXPLANATION OF PLATE 54

Spyridiophora distincta Cooper and Stehli, n. gen., n. sp. (p. 473)

FIGS. *1–17—1–4*, Respectively brachial, posterior, pedicle and anterior views of a strongly ornamented specimen preserving some of the long ear spines, ×1, paratype USNM 124116b; *5*, same specimen as preceding, ×2, showing ornamentation and ears in detail; *6*, another complete specimen, ×1, paratype USNM 124116a; *7–9*, respectively brachial, side and posterior views of the preceding paratype, ×2, showing reticulate ornamentation; *10*, side view of the same paratype showing spyridium and its supporting plates; *11*, interior of the pedicle valve showing ridges across ears, ear spines and granules on median surface, ×2, holotype USNM 124117; *12*, interior of a brachial valve showing the spyridium and cardinal process, ×2, paratype USNM 124116e; *13*, posterior view of the preceding specimen, ×3, looking into the spyridium, *14*, anterior view of the same specimen, ×2, showing plates supporting spyridium and defining cella; *15*, *16*, interior and posterior views of the brachial valve of the holotype showing the spyridium, median septum, subperipheral and brachial ridges, ×2; *17*, posterior of the same specimen showing closed spyridium, myophore and subperipheral flanges, ×4.

Permian (Wolfcamp formation, bed 9) at elevation 4700 feet on west side of hill 0.97 mile S. 82° W. of hill with elevation 5060 feet, Wolfcamp Hills, Hess Canyon (15 minute), Quadrangle, Texas.



Cooper and Stehli, Permian brachiopods, West Texas

PETRUNKEVITCH, Carboniferous *Trigonotarbus*, France

JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 475–477, PL. 55, 2 TEXT-FIGS., MAY 1955

TRIGONOTARBUS ARNOLDI, A NEW SPECIES OF FOSSIL ARACHNID FROM SOUTHERN FRANCE[1]

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ABSTRACT—*Trigonotarbus arnoldi*, n. sp., is described from the Carboniferous of southern France and compared with *T. johnsoni* Pocock, type species of the genus. The definition of the genus is emended by omitting from it mention of the eyes and eye-tubercle.

Genus TRIGONOTARBUS Pocock, 1911

THE Carboniferous arachnid order Trigonotarbi is rich in genera and species found both in Europe and in the United States. But the family Trigonotarbidae, characterized by the presence of only eight abdominal segments and the absence of marginal plates in the eighth tergite, is represented by a single genus *Trigonotarbus* and a single species, *T. johnsoni* Pocock (1911, pp. 73–75, fig. 38), apparently restricted to Great Britain. The characters of the genus were given by me in 1953 (pp. 89–90) as follows: "carapace triangular, high, with a pair of eyes on a tubercle, about half-way behind anterior end. Posterior end of abdomen evenly rounded." Of these characters the shape of the carapace is undoubtedly of generic value, as is the evenly rounded posterior edge of the abdomen. This qualification of generic characters is in harmony with their status in the closely related, but much richer family Eophrynidae in which the abdomen is always composed of nine segments, yet is evenly rounded in some genera, while in other genera its posterior edge has two pairs of spurs. The presence of an eye-tubercle is considered to be of generic or even familial value in some orders and the same applies to the eyes themselves and to the configuration of the eye group.

[1] A contribution from the Osborn Zoological Laboratory, Yale University.

But the absence of eyes in fossils may be accepted as a valid character only when there is sufficient evidence that it is not the result of poor preservation. Sessile eyes are often hard to see even when the surface of the carapace is smooth. This is not the case in *T. arnoldi*. The outlines of its carapace are quite clearly visible, but the surface is full of imperfections and of lines which in life did belong not to it, but to the ventral wall of the body. Although the eye-tubercle, on account of its nature and its position in the median line of the carapace, is usually recognizable even among other tubercles, its absence in *T. arnoldi* still could be accidental. I prefer therefore not to erect a new genus in absence of other specimens of the same species, but to amend my original definition of the genus *Trigonotarbus* by omitting from it the reference to the tubercle and the eyes and thus widening the scope of the genus sufficiently to include in it the new species.

The new species can be easily separated from the type species by the following characters:

T. johnsoni Pocock.—Size 4.7 to 6.5 mm. Carapace high, with an eye-tubercle bearing a pair of eyes situated about halfway between the anterior end and the posterior edge of the carapace. Abdomen about one and one-half times as long as the carapace and longer than wide.

T. arnoldi, n. sp.—Size 16.0 mm. Cara-

EXPLANATION OF PLATE 55

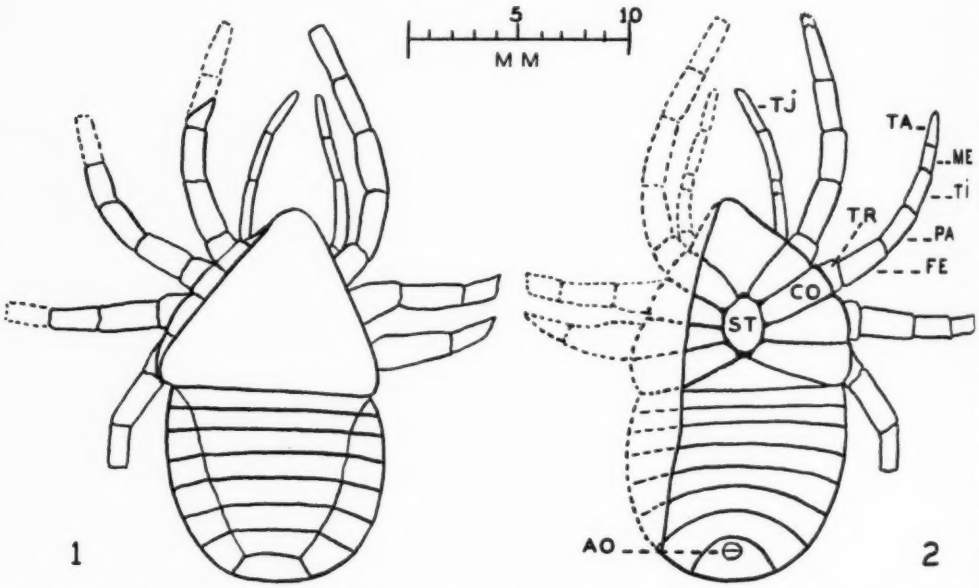
FIGS. *A*, *B*—*Trigonotarbus arnoldi* Petrunkevitch, n. sp. Holotype, Univ. Michigan, Mus. Paleontology No. 31602; middle Stephanian, Decazeville, southern France. *A*, Dorsal surface; *B*, ventral surface. Magnification as indicated by bar scale. (p. 476)

pace fairly flat, without a trace of either tubercle or eyes. Abdomen as long as carapace and wider than long.

TRIGONOTARBUS ARNOLDI Petrunkevitch, n. sp.
Pl. 55, figs. A, B; Text-figs. 1, 2

Holotype.—No. 31602 in the collection of the Museum of Paleontology, University of Michigan. Named in honor of Dr. Chester A. Arnold, Curator of Fossil Plants. Found at the top of the middle Stephanian at Decazeville in southern France.

Description of holotype.—Two pieces. Piece A (Pl. 55, fig. A) shows the dorsal surface of the animal with the lines of the sterno-coxal region superimpressed on the carapace, and the anal operculum similarly superimpressed on the eighth abdominal tergite. In Text-fig. 1 these ventral lines are purposely omitted. The carapace is somewhat distorted and the sterno-coxal wall of the cephalothorax slightly displaced, so that the ends of the coxae are visible on the left side, protruding from under the carapace as shown in the text-figure. In the specimen they are easily mistaken for the edge of the carapace, giving the latter a convex appearance. The lateral edge of the carapace is actually straight, but rather faint and visible only when the beam of light falls on it from the left side. The carapace appears then practically as an equilateral triangle with rounded corners, each side approximately 11 mm. long if one extends it to its intersection with the other two sides and disregards the rounded corners. In reality the sides are, of course, a little shorter and the actual length of the carapace in its middle line is only 8.0 mm. The surface of the carapace is uneven and the outlines of the sternum and of the pedal coxae are well visible. Moreover, the carapace is evenly punctate like the rest of the body, and where carbonized chitin is still preserved the surface is granular, each granule having the shape of a tiny hemipshere. There is no indication that the carapace may have been high, as it is in *T. johnsoni*, and while it may have been ornamented, no pattern of orna-



FIGS. *1, 2*—*Trigonotarbus arnoldi* Petrunkevitch, n. sp. Drawings of holotype. *1*, Dorsal surface with omission of all ventral lines. On the left side of the drawing the distal ends of the pedal coxae are shown protruding from under the carapace. The drawing represents piece A. *2*, Ventral surface as shown in piece B. The missing portion of the specimen is shown in dotted lines. AO—anal operculum, ST—sternum, CO—coxa, TR—trochanter, FE—femur, PA—patella, TI—tibia, ME—metatarsus, TA—tarsus, TJ—terminal joint of palp. Magnification as indicated by bar scale.

mentation can be discerned. Nor is there any trace of an eye-tubercle.

Piece B (Pl. 55, fig. B) shows the ventral surface with the outlines of the carapace superimpressed and clearly visible, but purposely omitted in the drawing (Text-fig. 2). The left quarter of the specimen is missing on piece B, and the missing parts are indicated in the drawing by dotted lines representing mirror images of the corresponding parts preserved on piece A. The pedipalpal coxae are not preserved. The pedal coxae are well visible and are of the type common to all Trigonotarbi, arranged around the sternum, in contact with each other. However, the relative width of sternum is visibly greater than in the type species.

The abdomen is 8.0 mm. long and 10.0 mm. wide (in the holotype of *T. johnsoni* it is 2.8 mm. long and 2.5 mm. wide). Since there is no indication that the abdomen in *T. johnsoni* may have been stretched either in life or in the process of fossilization, the difference in the proportions of the abdomen may be regarded as of specific value. Piece A shows eight tergites, all but the eighth divided into a median and a pair of marginal plates by two converging, longitudinal lines. Piece B shows eight sternites, all without marginal plates. The first sternite, limited on its sides by the fourth coxae, is triangular. On the eighth sternite a round anal operculum is present, divided by a transverse line into two halves.

The chelicerae are not visible on either piece, but both palpi are well preserved on piece A and the right palp can be seen on piece B to the base of its terminal joint. The palpi are considerably more slender than the legs and extend approximately as far as the end of the tibia of the first leg. Only the second right leg is complete. The first right leg is lacking its tarsus. The third right leg is preserved only to the end of its tibia and the fourth legs only to the end of their patella.

Lengths of appendages (mm.)

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	2.86	2.29	2.86	1.43	(?1.71)	11.15
II	2.43	2.14	2.71	1.29	1.71	10.28
III	2.29	2.29	2.57	?	?	?
IV	2.86	2.29	?	?	?	?

Palp: Femur 1.60, patella 0.70, tibia 2.10, terminal joint 2.20. Total length of palp 6.60 mm.

These measurements correspond in general to those in *T. johnsoni*, but in the latter the fourth femur is longer than the first femur and the total length of the fourth leg is greater than that of the first. The order of legs in *T. arnoldi* remains unknown for the present. The surface of the legs has the same appearance as that of the body. It may be assumed therefore that in life at least the entire dorsal surface of the animal was minutely granular. How much of the ventral surface was granular is difficult to determine, except in the case of the legs which were granular above and below.

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JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 2, PP. 478–509, PLS. 56–58, 1 TEXT-FIG., MAY 1955

EVOLUTION OF SANTONIAN AND CAMPANIAN *BELEMNITELLA* AND PALEONTOLOGICAL SYSTEMATICS: EXEMPLIFIED BY *BELEMNITELLA PRAECURSOR* STOLLEY[1]

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ABSTRACT—Evolution of Santonian and Campanian *Belemnitella* and the position of *B. praecursor* Stolley within their plexus are discussed. The plexus shows a complex evolutionary pattern consisting of the continuing, essentially irreversible, orthogenetic morphological changes of the whole stock coupled with and superimposed upon the relatively shortlived, essentially reversible (iterative), quantitative morphological shifts of its successive stages. Such a pattern appears to be widespread among the fossil invertebrate lineages. A critical taxonomical evaluation of this pattern leads to the conclusion that all quantitative morphological shifts belong to the subspecific or specific level; only the continuing orthogenetic changes should be given generic or higher rank. Most of the currently used, purely morphological, paleontological species and genera are of the lower level and so should be reduced in grade. A drastic simplification of the currently dominant, overrefined paleontological systematics is thus possible.

An extensive use of the "vertical taxonomy" at generic and higher levels and of the broad, "polytypic," paleontological species embracing all geologically contemporary, closely related and intergrading morphological forms is recommended wherever the material is ample. Otherwise open nomenclature should be most extensively used and the erecting of new species and genera avoided.

A paleontological species, as defined above, is believed to be a real, natural category for any given fraction of geological time, even though it represents but an artificial "slice" of a given plexus when a sufficiently complete lineage is studied through a considerable length of geological time. Waagen's mutations or chronological subspecies are denied any formal, taxonomical recognition, as they appear to be fully equivalent to paleontological species as here interpreted. Wherever necessary, an informal recognition of infraspecific, chronological phases as "high" and "low" forms of the given species is recommended instead of mutations.

All paleontological taxonomic categories are believed to be different from their neontological counterparts owing primarily to the omnipotence and the constant presence of the element of time in paleontology and its virtually total lack in neontology. The sharp contrast of static, morphological, and nonhistorical neontological classifications with the thoroughly dynamic, historical, and phylogentic paleontological classifications results therefrom.

Cryptogenic species and genera in paleontology are discussed and interpreted as a natural result of paleogeographical speciation and of the spacial restriction of the areas of evolutionary development of all fossil lineages. The forms representing "fragments" of such lineages outside of their evolutionary areas are quite naturally isolated and sharply defined morphologically in contrast to the plexi of the same forms within their evolutionary areas. Such an explanation is decidedly preferred to the assumption of abrupt, "macroevolutionary," genotypic jumps between species and genera, though these latter are not necessarily ruled out by the former concept. An analysis of *Belemnitella praecursor* Stolley, s. l., from the evolutionary, morphological, stratigraphical and paleogeographical points of view is chosen to illustrate the above conclusions. New paleontological varieties *B. p.* var. *media* and *B. p.* var. *mucronatiformis* are introduced. They, and most other morphological forms of the species, are figured.

It is demonstrated that all the hitherto known records of *B. praecursor* from outside its evolutionary area in the boreal Upper Cretaceous basin of European Russia lie well within the complete biozone (=total zone) of this species. The stratigraphically important concept of biozones versus partial paleontological zones is thus found to be valid in this particular instance, which is of a prime importance for long range (especially intercontinental or interprovincial) paleontological correlation.

[1] Published by permission of the Director-General of Scientific Services, Department of Mines and Technical Surveys, Ottawa, Canada. The Geological Survey of Canada accepts no responsibility for statements or conclusions appearing in this paper, which deals entirely with foreign fossil material.

Vorzüge des weitaus reicheren und vollständigeren Materials machen m.E. die Wirbellosen besonders geeignet auch zur Bearbeitung allgemein-paläontologischer bzw. -biologischer Fragen, die vielfach als eine Domane der Vertebraten-Paläontologie galten, bzw. als solche von ihr in Anspruch genommen wurden.—— O. H. Schindewolf (1944, pp. 670–671)

INTRODUCTION AND ACKNOWLEDGEMENTS

IN THE course of paleontological and stratigraphical research into Upper Cretaceous belemnites the writer became acutely aware of its evolutionary and taxonomic implications. Some of the writer's conclusions are presented in this paper. The importance of such an evolutionary and taxonomic study of a group of invertebrate fossils is considerably increased by the fact that the fossil invertebrates are in general very much neglected in this respect as compared with the fossil vertebrates. And yet, because of their comparatively small size, vast numbers, far simpler morphology, and often well preserved ontogeny, the fossil invertebrates are more suitable for evolutionary and taxonomic studies than any known group of vertebrates.

The paleontological record of the genus *Belemnitella* is complete enough for evolutionary treatment; it reveals a certain complex pattern that seems to be widespread among invertebrate lineages. The need to express taxonomically the evolutionary concept of this genus and of its species is responsible for a critical appraisal of certain taxonomic principles and practices widely accepted in modern paleontology. The study has, thus, provided an interesting opportunity for a practical application, at the specific and generic level, of nomenclatural, taxonomic, and phylogenetic principles advanced in a general form elsewhere (Jeletzky, 1950a).

It is earnestly hoped that the taxonomic approach advocated in this paper may be a step toward a mutually acceptable compromise between the practical taxonomic needs of the stratigraphic paleontologists, teaching paleontologists, and geologists and the taxonomic procedure of the majority of the modern evolutionary and museum paleontologists, which results in excessive splitting and grossly overcomplicated paleontological systematics.

At the specific level the present study is centered around *Belemnitella praecursor* Stolley, of which species the writer has studied extensive, well preserved, and stratigraphically reliable material. A detailed analysis of the other species discussed in the paper has been given elsewhere. Thus, the present study attempts to fill a considerable gap in our knowledge of *B. praecursor*. The Eurasian literature, indeed, lacks any work elucidating its essential morphological features, stratigraphical and paleogeographical range, and genetic relationships. This widespread and stratigraphically important species, is, moreover, still known under different names in various parts of its Eurasian realm, and satisfactory reproductions of its typical representatives and morphological varieties are scarce and scattered.

Special thanks are due to Dr. F. H. McLearn of the Geological Survey of Canada (retired) for the stimulating and helpful discussion of the general problems involved. Mr. A. G. Brighton of the Sedgwick Museum, Cambridge, England, lent the necessary comparative English material of *B. praecursor* Stolley and *B. mucronata* (Schlotheim). The writer gratefully acknowledges this loan and the permission to publish any of the Sedgwick Museum specimens. Sincere thanks are due to Dr. P. Harker, of the Geological Survey of Canada, Dr. E. Mayr of the American Museum of Natural History, New York and to Dr. John B. Reeside, Jr., of the United States Geological Survey, Washington, for reading the typescript and making valuable critical remarks, and to Mr. E. C. Elliott of the Photographic Division, Geological Survey of Canada for preparing all the photographs for this paper. Dr. John B. Reeside, Jr., has also kindly presented and sponsored this paper for publication.

EVOLUTION OF SANTONIAN AND CAMPANIAN *Belemnitella*

As far as known to date, *Belemnitella* forms ancestral to *B. praecursor* Stolley, s. l., are almost restricted to the so-called mid-Russian paleozoogeographical subprovince of the boreal province of the Upper Cretaceous sea of Eurasia. Only a few specimens of them have hitherto been recorded from Scania, Bornholm, and eastern and western

STAGES AND SUBSTAGES
STANDARD ZONES
BELEMNITE ZONES
RUSSIAN LOCAL ZONES
DIRECTIONS OF REVERSIBLE, QUANTITATIVE MORPHOLOGICAL SHIFTS
Towards
Strongly sculptured, mucronated forms
Smooth, non-mucronated forms
Towards
UPPER CONIACIAN
SANTONIAN STAGE
CAMPANIAN STAGE
Lower Campanian
Upper Campanian
Texanites emscheris and Inoceramus undulato-plicatus
Actinocamax lundgreni
Actinocamax lundgreni
Haenericeras clypeale, Placenticeras cf. guadalupe, In. cordiformis et var., Texanites texanus
Actinocamax westfalicus
Inoceramus pachti; Inoceramus cardissoides
Diplacmoceras bidorsatum, Haenericeras pseudogardeni, Scaphites bartlingi
Pachydiscus dulmensis, Scaphites aquisgranensis, S. binodosus, S. hippocrepis
Hoplitoplacenticeras vari and Hamites phaleratus
Bostrychoceras polyplocum and Pachydiscus oldhami
Marsupites spp., Uintacrinus spp. (in the lower subzone.) Bohmoceras spp., Placenticeras syrtale
Gonioteuthis granulata f. ant., Gonioteuthis westfalica-granulata (in the lower subzone)
Gonioteuthis granulata f. typ., G. granulato-quadrata
Gonioteuthis quadrata et var.
Belemnitella mucronata mut. senior s. str., B. mucronata
Belemnitella mucronata mut. minor, B. langei s. str.
Pteria tenuicostata
Belemnitella mucronata
Belemnitella propinqua
Belemnitella ex gr. mirabilis
Belemnitella ex aff. mucronata
Belemnitella sp. nov. praecursor
Belemnitella praecursor var. praecursor
Belemnitella praecursor var. media nov. var.
Belemnitella praecursor var. mucronatiformis nov. var.
Belemnitella lanceolatus Sharpe non Schloth. 1813
Belemnitella nov. sp. aff. mucronata
Belemnitella mucronata var. (unnamed slender variety)
Belemnitella mucronata mut. senior
Belemnitella langei
Belemnitella mucronata mut. minor
Belemnitella senior mucronata mut. senior
"low" forms of B. praecursor
"high" forms of B. praecursor
stratigraphical range of B. praecursor
The range of variation in sculpture and character of apical end of the guard characteristic of B. praecursor and earlier forms
The range of variation in the same characters characteristic of B. ex gr. mucronata of Upper Campanian
Direction of irreversible orthogenetic trends (gradual calcification and deepening of preserved alveolus, gradual intensification of sculpture of the guard and its mucronation, gradual formation of calcified, pitted and tuberculated, thick conotheca and its transformation into smooth, thin conotheca of Upper Campanian Belemnitella-forms, etc.).
G.S.C.

Direction of irreversible orthogenetic trends (gradual calcification and deepening of preserved alveolus, gradual intensification of sculpture of the guard and its mucronation, gradual formation of calcified, pitted and tuberculated, thick conotheca and its transformation into smooth, thin conotheca of Upper Campanian *Belemnitella*-forms, etc.).

G.S.C.

Prussia. However, it is quite possible that the paleogeographical range of all ancestors of *B. praecursor* included most or all of the Baltic region and that scarcity of records there is due only to the nearly total lack of exposures of the corresponding Upper Cretaceous strata (Jeletzky, 1949b, p. 423). From the distribution, and from the observed intergradation of older forms of *Belemnitella* with *B. praecursor* Stolley in European Russia, it appears that the early evolutionary development of the genus *Belemnitella* took place in the Russian basin of the Upper Cretaceous boreal province of northern Eurasia (Jeletzky, 1948b, pp. 593–595; 1949b, pp. 418–423; 1950a, p. 33, fig. 2; 1951b, pp. 83–85). Its course will be discussed below, and the author's conclusions are reproduced diagrammatically in Text-fig. 1.

Personal observations (Jeletzky, 1948b, pp. 593–595, Beilage 1;1949b, pp. 418–419, 422; 1951b, pp. 84–85) indicate that *B. praecursor* is a direct descendant of a hitherto undescribed Santonian primitive form, which was temporarily designated *Belemnitella* ex gr. *B. mirabilis* Arkhangelsky, 1912 (Jeletzky, 1949b, p. 422) but seems to be synonymous with *B. mucronata* (Schlotheim) mut. *anterior* of Stolley (1897, pp. 296–297) from Eriksdal in Scania. It is, indeed, very similar to "*?Actinocamax propinquus*" of Moberg (1885, pl. 6, fig. 22, non pl. 5, fig. 25), which is the only hitherto published specimen of *B. mucronata* mut. *anterior*. A typical specimen of *B.* ex gr. *B. mirabilis* is reproduced on Pl. 58, fig. 5a–d.

In the vicinity of the towns of Rylsk and Novosybkov on the northeastern slope of Dniepr-Donetz depression in southwestern Russia, the glauconitic-sandy marls, lying between the beds with *B.* ex gr. *B. mirabilis* and the overlying clayey marls with *B. praecursor* Stolley, *Gonioteuthis granulata* (Blainville) f. typ., *Actinocamax verus* Miller var. *fragilis* Arkhangelsky, and rare *Belemnitella* ex gr. *B. mucronata* (here renamed *B. praecursor* Stolley var. *mucronatiformis*, n. var.) (see Jeletzky, 1948b, Beilage 1), do not seem to carry *Belemnitella* ex gr. *B. mirabilis*. A small, slender, smooth to feebly sculptured *Belemnitella*, temporarily designated *Belemnitella* n. sp., aff. *B. praecursor* Stolley, and clearly intermediate in all its morphological features between the older *B.* ex gr. *B. mirabilis* and the younger *B. praecursor*, occurs there. Together with it there was found another new form of *Belemnitella* which will be temporarily designated *B.* ex aff. *B. mucronata* (Schlotheim); it is also small, slender, more or less lanceolate, and moderately to feebly sculptured. It possesses, however, a blunter apical end of the guard with a more distinctly separated mucro, and a longer ventral fissure than either *B. praecursor* or *B.* n. sp., aff. *B. praecursor*. The bottom of the ventral fissure of *B.* ex aff. *B. mucronata* is more or less bent and forms a larger angle with the inner wall of the alveolus than in *B. praecursor* Stolley.

In so far as *B.* n. sp., aff. *B. praecursor* and *B.* ex aff. *B. mucronata* are very similar morphologically, occur in the same beds, and intergrade with one another, they are hardly more than morphological varieties of one and the same, hitherto undescribed, new species. Yet they deserve attention, since they appear to represent the earliest record of morphological divergence in the *Belem-*

FIG. 1.—Evolution of Santonian and Campanian *Belemnitella* in the boreal basin of European Russia.

The diagram should not be interpreted as strictly quantitative. In some instances technical considerations have necessitated pronounced discrepancies. Thus the width of the space allocated to *B. praecursor* Stolley var. *mucronatiformis*, n. var., during the time of *Diplacmoceras bidorsatum* should be narrowed to at least one-third of its width in the diagram and that allocated to *B. praecursor* Stolley var. *media*, n. var., should be widened accordingly. The width of space allocated to *B. mucronata* (Schlotheim) mut. *senior* Nowak, s.s., during the time of *Hoplitoplacenticeras vari* should at least be doubled, as this form makes up from 50% to 75% (sometimes even more) of the *Belemnitella* populations of that time.

Representatives of most of the species and infraspecific forms covered by this diagram are illustrated in Pls. 56–58.

The outlines of the *Belemnitella* plexus, and ranges of its individual species and infraspecific forms are shown by solid lines.

Maestrichtian species of *Belemnitella* are not considered. Also the still somewhat doubtful occurrences of *B. junior* Nowak, s.s., in the beds of uppermost Campanian age (e.g., on the north border of the Donetz basin) are ignored.

nitella-plexus. They both appear to be immediate descendants of the earlier *B.* ex gr. *B. mirabilis* Arkhangelsky, but they seem to transmutate into two morphologically distinct forms in the immediately overlying beds. *B.* n. sp., aff. *B. praecursor* appears to grade into average forms of *B. praecursor* described below as *B.p.* var. *media*, n. var., while *B.* ex aff. *B. mucronata* appears to transmutate directly into very similarly sculptured, mucronated forms, described below as *B. praecursor* var. *mucronatiformis*, n. var. This latter coexists in small numbers with *B. praecursor* var. *media*, n. var., throughout the vertical range of the species. *B. praecursor* var. *mucronatiformis*, and the still undescribed *B.* ex aff. *B. mucronata* from the upper part of *cardissoides* beds of Dniepr-Donetz depression (see Jeletzky, 1948b, Beilage 1, column 1), are more strongly sculptured, more mucronated, and possess a longer ventral fissure than either *B.* n. sp., aff. *B. praecursor* or the younger *B. praecursor* var. *praecursor* and *B.* var. *media*. They were discussed in considerable detail elsewhere (Jeletzky, 1951b, pp. 83–85).

The number of specimens of all the new *Belemnitella* forms discussed above, collected by the writer layer by layer on the northeastern slope of Dniepr-Donetz depression, is not quite sufficient to prove the above conclusions by the observation of their gradual intermutation into one another step by step in the ascending succession of beds. Yet the morphological drawing together of all these forms and their respective stratigraphical positions in the sections make the phylogenetical conclusions presented above sufficiently reliable, at least in their general outline.

Previously it was assumed that *B. preacursor* Stolley, s. l., can hardly be an immediate evolutionary link between *B.* ex gr. *B. mirabilis* Arkhangelsky (?=*B. mucronata* Schlotheim mut. *anterior* Stolley, 1897) and the typical *B. mucronata* of the upper Campanian. It rather seemed to be a short-lived offshoot of the main stem (plexus) of this genus (Jeletzky, 1948b, pp. 593–595; 1949b, pp. 418–419; 1951b, pp. 83–85). For this very reason *B. praecursor* was omitted altogether from the diagrammatic scheme of evolution of the genus *Belemnitella* published by the writer (1950a, p. 33, text-fig. 2).

The circumstance, however, that throughout the stratigraphical range of *B. praecursor*, s. l., hosts of *B. praecursor* var. *media*, n. var., appear to link the extreme smooth forms of *B. praecursor* var. *praecursor* with the contemporary representatives of *B. praecursor* var. *mucronatiformis*, n. var., indicates, in the opinion of the writer, that they all are only morphological varieties of the same specific type (parts of the same populations; Jeletzky, 1950a, p. 23). *B. praecursor* var. *praecursor* and *B.p.* var. *mucronatiformis* occupy, so to speak, the fringes of the same plexus, the axial part of which was occupied by *B. praecursor* var. *media* (see Text-fig. 1).

B. praecursor, s. l., apparently arises out of *B.* n. sp. aff. *B. praecursor* Stolley and *B.* ex aff. *B. mucronata* (Schlotheim), which in certain characters are morphologically closer to the upper Campanian forms of *B. mucronata* (Schlotheim) than to the former species. Shortly after its first appearance the segment of the plexus occupied by *B. praecursor* var. *praecursor*, *B. praecursor* var. *media* and the intermediate forms between this latter and *B. praecursor* var. *mucronatiformis* becomes, geologically speaking, rapidly expanded almost to the exclusion of *B. praecursor* var. *mucronatiformis*. The strong predominance of these two varieties of *B. praecursor*, s.l., which together comprise up to 90–95% of the forms of *Belemnitella* in the populations of latest Santonian and earliest Campanian time, persists at least through the lower part of the *P. tenuicostata* zone (=zone of *Diplacmoceras bidorsatum*). Higher in the succession of beds the hitherto rare *B. praecursor* var. *mucronatiformis*, n. var., begins to increase markedly in populations of *B. praecursor*, s.l., at the expense of *B.p.* var. *media*, n. var., and especially of the extreme, smooth forms close to *B.p.* var. *praecursor*. At the same time *B. praecursor* var. *mucronatiformis*, n. var., gradually transmutates into slender, unnamed varieties of *B. mucronata* (Schlotheim) and into *B. mucronata* (Schlotheim) mut. *senior* Nowak.

The smooth to feebly sculptured, essentially nonmucronated *Belemnitella* of the type of *B. praecursor* Stolley, s.l., become rare at

the close of the *P. tenuicostata* time (=uppermost lower Campanian), at which time the strongly sculptured, mucronated *B. mucronata*, s.l., begins to dominate strongly the *Belemnitella* populations. *B. mucronata*, s.l., and *B. junior* Nowak dominate the *Belemnitella* plexus throughout upper Campanian and Maestrichtian epochs. More details about the evolution of the *Belemnitella* plexus during the time of predominance of the type *B. praecursor* Stolley have been given elsewhere (Jeletzky, 1951b, pp. 83–85).

The phase of the pronounced predominance of *B. praecursor*, s.l., appears therefore to be inserted between two phases of domination of more strongly scuplptured and mucronated *Belemnitella* forms, and thus to be but a temporary and generally reversible phase of the evolution of the *Belemnitella* plexus. The next, even more pronounced, but morphologically opposite, phase of predominance of *B. mucronata* (Schlotheim) mut. *senior* Nowak, s.s., (Jeletzky, 1951b, pp. 83–85; this paper, Text-fig. 1) appears to be an equally temporary and generally morphologically reversible evolutionary phase of the same plexus. Already in the *Bostrychoceras polyplocum* zone of the upper Campanian substage, *B. mucronata* mut. *senior* is replaced by much more slender and partly considerably less mucronated (though predominantly sufficiently strongly sculptured) *B. lanceolatus* Sharpe non Schlotheim, *B. mucronata* mut. *minor* Jeletzky 1951 and *Belemnitella*, n. sp., aff. *B. mucronata* (?=*B. lundgreni* Morgan, 1882). Especially a temporary but pronounced phase of predominance of *B.*, n. sp., aff. *B. mucronata* of Jeletzky (1948b, pp. 597–599, text-figs. 1 and 2) in the middle part of the upper Campanian substage is similar to that of *B. praecursor* Stolley, s.l., in the lower Campanian. Phases of predominance of *B. mucronata* mut. *minor*, *B. langei* Jeletzky, 1948, and finally that of *B. junior* Nowak, s.s., in the Maestrichtian, present other examples.

The evolutionary development of the *Belemnitella* plexus appears therefore to consist of a series of pronounced, but generally short lived and reversible, shifts in morphological appearance of forms of *Belemnitella*, which dominate its successive stages. These changes in morphological appearances are herewith termed "reversible quantitative morphological shifts." They are, however, coupled with and superimposed upon more general and lasting morphological changes of the whole stock, which form generally irreversible, orthogenetic trends progressing in one and the same direction in the course of geological time. These latter trends are exemplified by the gradual, irreversible deepening of the calcified, preserved part of the alveolus during the earlier evolutionary stages of the *Belemnitella* plexus caused by an equally gradual calcification of the alveolar part of the guard in these forms in the course of their phylogeny (Jeletzky, 1948a, pp. 229–232; 1949b, pp. 418–419). This trend is also operative in the *Gonioteuthis* and *Belemnella* plexi. Gradual, generally irreversible, intensification of the sculpture of the guard; somewhat more reversible, gradual lengthening of the preserved ventral fissure; gradual intensification of the mucronated, obtuse appearance of the apical end of the guard; and the irreversible phylogenetic changes of the conotheca discussed below, all belong in this category. There is, however, no sharp natural boundary between the two kinds of evolutionary changes and they are so tightly interwoven as to admit only of an approximate and somewhat arbitrary delimitation.

Most of these irreversible trends were operative only during certain stages of the known duration of the *Belemnitella* plexus. The increase in the relative depth of the alveolus, for example, virtually ceased in the early upper Campanian, when it reached about half of the total length of the guard in typical *B. mucronata* (Schlotheim), s.l. The complete calcification of the alveolar part of the guard was already achieved in the lower Campanian in *B. praecursor* Stolley, s.l.

Gradual intensification of the sculpture of the surface of the guard is, however, an exception, since the last known members of the genus *Belemnitella*, s.s.—*B. junior* Nowak, s.s., in Eurasia and *B. americana* (Morton, 1830) non Arkangelsky, 1912, in North America—are its most strongly sculptured representatives. The same is true of the gradual changes of the conotheca (see below).

The multitude of different morphological forms encountered at every evolutionary stage of the *Belemnitella* plexus is due, in the writer's opinion, to the countless possible, and achieved, morphological combinations produced by the interaction of lasting orthogenetical trends with the repeated, reversible, quantitative shifts in the morphological appearance of paleontological populations at each consecutive evolutionary stage.

RECAPITULATION OF ANCESTRAL CHARACTERS IN *Belemnitella*

The writer has pointed out on several occasions (Jeletzky, 1949a, pp. 270–277, 279–283; 1951b, pp. 81–127) that evolutionary changes of quite a few morphological features of *B. praecursor* Stolley, s.l., its ancestors and descendants, and the other evolutionary trends of Belemnitellidae as well, follow the mode of phylembryogenesis for which the term "anaboly" was introduced by Sewertzoff (1912, 1925, 1927, 1931, pp. 266–277; 1939, pp. 483–505). Such changes are also known as "tachygenesis," "hypermorphosis," and "acceleration" (e.g., de Beer, 1940, pp. 29, 65–77) and represent a widespread, if not universal, mode of phylembryogenesis, rather useful both phylogenetically and stratigraphically (Jeletzky 1950a, p. 26).

The similarity of the sculpture and of the general outline of the guard of the earlier growth stages of *B. mucronata* (Schlotheim), s.l., and in particular of those of *B. mucronata* mut. *senior* Nowak, s.s., to the adult stages of *B. praecursor* Stolley, s.l., presents an example of anaboly (Jeletzky, 1951b, pp. 82–83). The same mode of evolutionary change is apparent in the gradual complication of the outline of the bottom of the ventral fissure in *B. mucronata*, s.l., and in *B. junior* Nowak, s.s.

One more example of development according to the mode of anaboly is given by the evolutionary changes of the conotheca of the phragmacone in the *Belemnitella* plexus. This was partly discussed elsewhere (Jeletzky, 1949b, pp. 418–419). Indeed, the whole surface of the conotheca of *B. propinqua* (Moberg) and *B.* ex gr. *B. mirabilis* Arkhangelsky is strongly ornamented by coarse and prominent tubercles, irregular pits and furrows. This ornament is much more pronounced in the adult stages of growth than in the juvenile stages (Jeletzky, 1949b, text-figs. 1, 2c-d, 3a-b, 4; this paper Pl. 58, fig. 5c-d). In *B.*, n. sp., aff. *B. praecursor* Stolley the average size of these tubercles, pits and furrows is greatly diminished (they are visible to the naked eye only upon close scrutiny). These elements of the ornament are only slightly coarser in the adult stages of ontogeny than in its early stages. The adult stages of ontogeny of the early forms of *B. praecursor*, s.l., show in most cases only a slightly sculptured conotheca, whereas its ornament in the earlier ontogentic stages is much more pronounced (see Pl. 56, fig. 4). In the later forms of *B. praecursor*, s.l., the ornamented conotheca is in most cases present only in the earliest stages of ontogeny, being pushed farther and farther back in the terminology of recapitulationists, and gradually decreasing in prominence at the same time. Adult and adolescent stages of ontogeny in these forms show only faint vestiges of ornament, (see for example the specimens figured on Pl. 57, fig. 2c and Pl. 58, fig. 1c). A fair number of guards with practically smooth conothecas begins to appear here, though more strongly sculptured conothecas still occur in a small number of specimens. The earlier forms of *B. mucronata* (Schlotheim), s.l., and in particular *B. mucronata* mut. *senior* Nowak, s.l., have even smoother conothecas, though a distinct ornamentation is still present in the earliest ontogenetic stages. In the later morphological forms of *B. mucronata*, s.l., a practically smooth conotheca is the rule. Even under a binocular one seldom observes the vestiges of the ornamented conotheca in the earliest stages of the ontogeny of these forms. The last stage of the *Belemnitella* plexus (*B. junior* Nowak, s.s.) has the smooth, non-sculptured conotheca even in the earliest stages of ontogeny, and the writer does not know of any exceptions.

GENERAL EVOLUTIONARY AND TAXONOMIC REMARKS

The following general remarks constitute an attempt at an evolutionary and taxonomic appraisal of the results presented above. At the same time they are intended to elucidate the principles followed in the treatment of *B. praecursor* Stolley, s.l., in

the systematic part of this paper. The writer (Jeletzky, 1948a, pp. 230–232; 1949b, pp. 418–419) has shown that most of the plexi of the Belemnitellidae known to date have evolved in the same general direction and along parallel lines with the *Belemnitella* plexus. In this respect the evolution of the Belemnitellidae presents just one more example of that particular variant of orthogenetic evolution which was designated "programme evolution" (Lang, 1923) or "Typostase" (Schindewolf, 1947, p. 16; 1950b, pp. 229, 238–239). An elaborate discussion of "programme evolution," as exemplified by the Graptoloidea, was given by Bulman (1933).

The intertwining of the above mentioned lasting orthogenetic trends with essentially reversible, quantitative shifts in the *Belemnitella* plexus and the resulting complex pattern of its evolutionary development do not seem to be a generally recognized phylogenetical phenomenon. And yet they seem to be of considerable theoretical and practical importance, being apparently a rule rather than an exception. The writer has indeed observed exactly the same pattern in other plexi of the Belemnitellidae (not yet published) and also during his unfinished studies of Canadian *Scaphites* and *Aucella*. It seems likely that Riedel (1931, p. 610) referred to a similar phenomenon, when he wrote about the flucto-mutational lineage of *Gonioteuthis westfalica-quadrata*, though he did not explain the exact meaning of this term. Tripp, Schwegler and Zoch (references in Jeletzky, 1949a, pp. 260–261; 1950a, p. 27) have definitely encountered it in Jurassic Belemnitacea. Arkell (1950, pp. 356–357) has described an evolutionary pattern of this type in his comments on the evolution of Jurassic Perisphinctacea. Finally, Joysey (1952) has recently discussed a theoretical case of an apparently similar pattern.

The difficulties of expressing such complex patterns of invertebrate plexi in terms of conventional taxonomic units are clearly discernible in the doubts which Arkell (1950, pp. 356–357) expressed with regard to the possibility of "a logical classification of Perisphinctacea." After an able discussion of the various "kinds of evolutionary changes" in the Perisphinctacea, Arkell reached the conclusion that: "Criteria of the second kind [changes in the main stock] are the only ones reliable for dating." Thus, he has clearly recognized the higher evolutionary, and accordingly taxonomic, value of the lasting changes of the stock designated by the writer as orthogenetic trends. Yet Arkell ends the argument with a completely resigned statement:

> It is a fault for which no remedy is apparent, that these cross-sections of the main stock, or "column-drum" divisions, should have to be equated with the "dead-end" offshoots as equal taxonomic units.

The writer, however, would argue, contrary to Arkell that such a complex nature of evolutionary patterns in paleontology may, and should, be used for simplification and drastic downgrading of the over-complicated and impractical taxonomic systems produced by many modern paleontologists, especially by modern ammonitologists. He believes that the tendency to "split," characteristic of modern paleontologists, is caused, partly at least, by their failure to recognize this complex nature of the evolutionary patterns of fossil lineages. Equating all kinds of evolutionary changes observed, such authors tend to express in terms of conventional taxonomic units and to name as species individuals possessing even the finest morphological distinctions without due regard to their intergradation or the stability of their morphological distinctions in time and space. This attitude may also well be caused by the widespread but unfortunate feeling that a species is an essentially morphological, static and at the same time smallest recognizable taxonomic category. This concept appears to have been introduced by d'Orbigny and Oppel (see Holder, 1952, pp. 272–273) and is definitely derived from the older neontological systematic principles now often refuted by neontologists themselves (e.g. Huxley, 1940; Rensch, 1929; Mayr, 1944, 1952).

The temporary and essentially reversible, quantitative "shifts" should, in the opinion of the writer, under no circumstances be taxonomically equated with the lasting, "irreversible," orthogenetic evolutionary changes of the same stock. The former appear, indeed, to be mere paleoecological adaptations, which expressed essentially, or even completely, the phenotypic rather than

genotypic changes of the stock. It is, accordingly, proposed either to deny any formal taxonomic recognition to these inferior evolutionary changes or to recognize them only at subspecific level. In the most pronounced instances, especially when specific or generic names have already been given to forms exhibiting such shifts, they might perhaps be regarded as species, but certainly not as genera or subgenera. Their adequate description and illustration are naturally considered obligatory. Specific rank should normally be given only to complete, three-dimensional, evolutionary stages of plexi such as *B. praecursor* Stolley, s.l., or *B. mucronata* (Schlotheim), s.l., including all contemporary morphological "shifts," however pronounced they may be. The writer (see Jeletzky, 1951b, p. 38) has already pointed out, contrary to Simpson (1940, p. 414), that such broad paleontological species are not artificial and subjective concepts but are separated by clear-cut, morphological gaps from any contemporary species, as all closely related, contemporary forms intergrading with one another are by definition included in one species. Only the "bottom" and "top" limits of paleontological species so defined remain subjective. These limits would naturally have to be drawn as artificial, horizontal cuts through the uninterrupted evolutionary streams of forms wherever the paleontological record of the given group of fossils is complete or almost complete. These artificial, horizontal cuts (Jeletzky, 1950a, pp. 24–25) should, whenever possible, be undertaken with due regard to the already existing nomenclature. From a paleobiological standpoint (see Jeletzky, 1950a, p. 24; Simpson, 1951) such species names may appear unnecessary, as long as the course of the plexus is sufficiently well known. Its whole known length could, indeed, be called one species, were it not for the practical needs of biostratigraphers. Maximum attention should therefore be paid to the creation of stratigraphically useful species, wherever such artificial, horizontal cuts through the plexus are undertaken.

All forms distinguishable within the known stratigraphic range of a given plexus should be placed in the same genus or subgenus (so-called vertical genera; see Simpson, 1945) unless the stock is known to be very long lived and changes so strongly in the course of its development as to justify cutting it into two or more sections, each consisting of at least several paleontological species as defined above. Otherwise, such cuts should preferably be made at places where long-lived offshoots of the main plexus branch off. Offshoots of this type may naturally be given generic or subgeneric rank, in contrast with the much more numerous, short-lived morphological shifts discussed above.

As a rule it seems safe and profitable for paleontologists to accept the principle that not more than one broad paleontological species should be recognized among one or many samples of paleontological populations collected from the same narrow bed or horizon (regardless of the distance between outcrops), provided that their extreme morphological members are close enough to assume that they would intergrade with one another, if a large enough series were collected. When such a series is available and the end forms really do intergrade, it is quite inexcusable to give them anything but subspecific rank. Most of the modern paleontological species, and a great many genera, are nothing more than morphologically distinct, contemporary forms (paleontological varieties) of the same broad species (Mayr, 1952, p. 449). Most of the ammonoid species and genera of Spath (1927–1933, 1923–43) and Buckman (1909–1930) and the inoceramid species and genera of Heinz (1932) are of this nature. This is often frankly admitted (e.g., Spath 1923–43, p. iii-v, and elsewhere), but such procedure is commonly defended as practically useful (e.g., Weller, 1950; McKerrow, 1952). The writer, however, completely agrees with the criticisms directed against such a procedure by Rowe (1899, pp. 495–498, 541–544) (see also Stolley, 1911, pp. 7–10; Wright, 1950; Simpson, 1951; Sylvester-Bradley, 1952, p. 230; Mayr, 1952, p. 449; and Weller, 1952). It seems that the only way to remedy this practice is to adopt the broad evolutionary concept of the paleontological species, as defined above, to which the term "polytypic species" of Huxley (1940, p. 10) was applied by Haas (1946, pp. 147–148). The practical needs of biostratigraphers, which

constitute the trivial excuse for a very narrow concept of paleontological species (e.g. Diener, 1925, pp. 143–144), can be easily reconciled with the concurrent use of broad polytypic species. One has only to "slice" his plexi into the maximum possible number of chronologically subsequent paleontological species, combined with ruthless downgrading of all contemporary and intergrading forms to varieties or paleogeographical subspecies.

Extreme and mean morphological forms of a given polytypic paleontological species (in our case those of *B. praecursor* Stolley, s.l.) normally occur together at the same fossil localities and more or less throughout its stratigraphical range. Therefore they represent parts of the same paleontological population and should be referred to as morphological varieties and not as subspecies of any kind (see Jeletzky, 1950a, p. 23).[1] Naturally the percentages of such paleontological varieties may vary within wide limits at different localities and in different parts of the stratigraphical range of any given paleontological species. In themselves they do not reflect any subspecific evolutionary stages (chronological subspecies or Waagen's mutations) of the latter, being mainly vertical cuts through a given evolutionary phase of the plexus that corresponds to a paleontological species and is separated above and below by imaginary, conditional limits from ancestral and descendant species.

Paleontological species do not remain static throughout their stratigraphical ranges but change gradually all the time (Rowe 1897, pp. 495–498; Stolley, 1911, pp. 7–10; Elias, 1936, p. 374); this circumstance provides the basis for their subdivision into chronological subspecies, which, although chronologically opposed to the paleontological varieties, are very tightly interwoven with and arise out of them (Jeletzky, 1950a, p. 23). Hitherto the writer has designated formally such chronological subspecies, representing a complete "slice" (phase) of a plexus, as Waagen's mutations (Jeletzky, 1949a; 1950a, pp. 22–25; 1951b, pp. 80–127). Now he feels, however, that, as pointed out by McKerrow (1952), such a concurrent use of formally named contemporary paleontological subspecies, varieties and mutations (=chronological subspecies) within every polytypic paleontological species is inconvenient in overburdening the nomenclature. Indeed, the mutations are taxonomically superior to paleontological varieties (Jeletzky, 1950a, p. 23), and one would have to recognize a set of these latter not only for each species but also for each successive mutation. The writer's revised taxonomic procedure is, furthermore, in agreement with the currently predominant practice of invertebrate paleontologists, which certainly is not the case with the mutations (=chronological subspecies). Therefore it seems to be more practical to give the rank of paleontological species to every morphologically discernible evolutionary stage of the plexus and so to substitute the sequence of paleontological species for the sequence of mutations. Whenever it is undesirable to "split" the plexi into extra-thin "slices" of formally named paleontological species, informally named "high" and "low" morphological forms (mutations) may be recognized within each broader paleontological species, following the example of Stolley (1897; 1911, pp. 7–10) and other authors. This is done here for *B. praecursor* Stolley, s.l. (see Text-fig. 1 and later pages of this paper).

Naturally, the above procedure can be followed only when the paleontological material is complete enough for reconstruction, or for the investigation, of at least one evolutionary stage of the plexus. Such cases are far more numerous than a survey of modern paleontological literature would lead us to believe, yet it must be freely admitted, with Haas (1942, pp. 6–7) and McKerrow (1952), that in a great many cases paleontological material is unfit either for recognition of its evolutionary patterns or

[1] Until recently the term variety, though widely used in invertebrate paleozoology, did not have any legal status under the International Rules of Zoological Nomenclature and some invertebrate paleontologists have objected to its use. The acute need for such a noncommittal subspecific term in paleozoology (as opposed to neozoology) has been finally recognized by the Copenhagen Colloquium on Zoological Nomenclature (see Copenhagen Decisions on Zoological Nomenclature; Additions to, and Modifications of, the Regles Internationales de la Nomenclature Zoologique, Edited by F. Hemming, London, 1953, p. 84). Henceforth no legal objection can be made to the use of the term variety (or variant), as employed above, by paleozoologists.

even for its taxonomical treatment according to the principles advocated above. In all such cases, however, a complete abstention from introduction of new names, or from any broad evolutionary generalizations, combined with the most extensive use of open nomenclature, are the only advisable means (see Jeletzky, 1950a, pp. 22–25). As long as such a strictly conservative taxonomical attitude is maintained, the fact that the paleontologist at the outset, and even at the advanced stages of his research, often does not know much about the real nature of his species and higher taxonomic units (Simpson, 1951, pp. 296–297) gives no reason for "splitting." The thesis of Wright (1950, p. 748) that "genera and species are bound to proliferate in the analytical phase of the study of the group" is therefore rejected emphatically and the writer thinks with Rowe (1899) and Stolley (1897, 1911) that this proliferation should never happen, even though, unfortunately, it has happened in too many instances in the past. Excellent examples of the broad evolutionary treatment of paleontological species and their infraspecific variation, which agree exactly with the principles advocated above, are

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EXPLANATION OF PLATE 56

All figures natural size unless otherwise indicated

FIGS. *1–3*—*Belemnitella praecursor* Stolley var. *media* Jeletzky, n. var.; schematic drawings showing the outline of the bottom of the ventral fissure. *1*, specimen B-65347, illustrated on Pl. 57, fig. 3. *2*, holotype, illustrated on Pl. 57, fig. 4. The outline of the bottom of the ventral fissure is typical of the average ("mean") morphological form of the species. *3*, specimen B-65346, illustrated on Pl. 58, fig. 4. Like the specimen shown on Pl. 56, fig. 1, the outline is characteristic of "high" forms of the species. (p. 497)

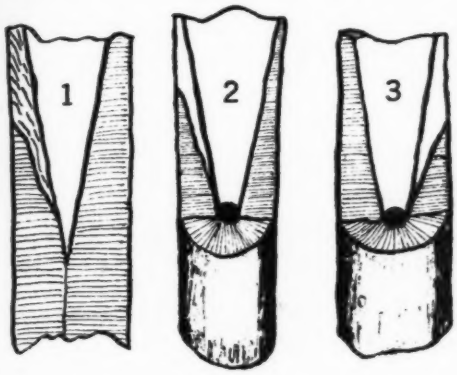
4—*Belemnitella praecursor* Stolley, s.l. Inside view of the alveolus of a specimen from an unknown locality, ×4. Note the distinct ornamentation of the surface of the conotheca near the apex of the alveolus. The area covered with this ornamentation, consisting of tiny rounded tubercules and pits, extends from the embryonic bulb to the beginning of the ventral fissure on the inner wall of the alveolus. The coarsest tubercles and pits are restricted to the smaller area immediately above the embryonic bulb. In the higher parts of the alveolus the surface of the conotheca becomes nearly smooth within a few millimeters above the beginning of the ventral fissure. (p. 491)

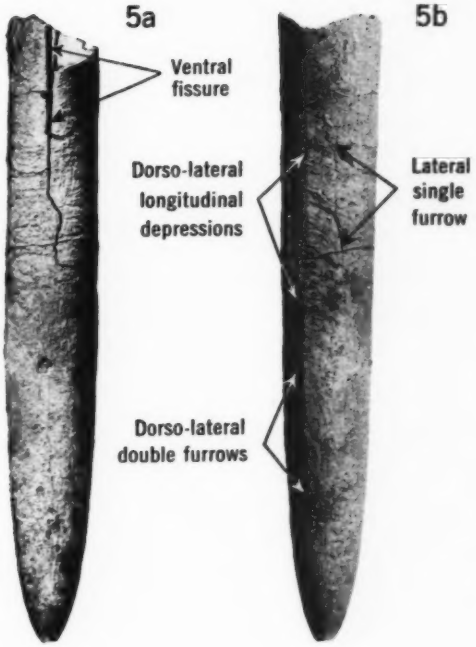
5a–d—*Belemnitella praecursor* Stolley var. *mucronatiformis* Jeletzky, n. var. Holotype, University of Cambridge, Sedgwick Museum coll. no. B-66985. Upper Chalk, *quadrata* zone in the broad sense (lower Campanian), East Harnham, Wiltshire, England. Collected by R. M. Brydone; ex Dr. Blackmore collection. *a*, *b*, Ventral and lateral views. *c*, Lateral view with the alveolar part split off to show the inside of the alveolus, its depth, outline, ventral fissure (Schatsky index is 10.0–10.5 mm. on original), and the form of the bottom of the ventral fissure. *d*, Schematical drawing of the alveolar part of the other half of the guard, showing in a somewhat overstressed form the wavering of the bottom of the ventral fissure. The most important morphological elements of the *Belemnitella* guard discussed here, and in the text of the paper, are indicated on the figures.

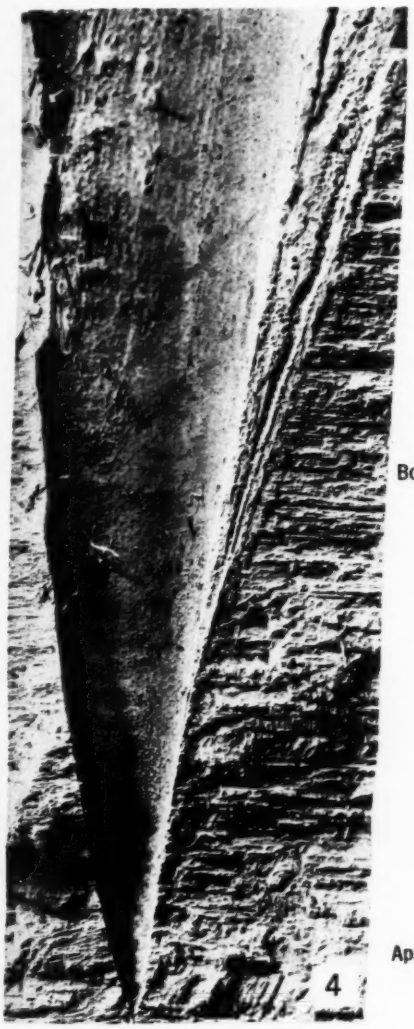
This guard, small, slender, and somewhat lanceolate ventrally, is typical of this extreme variety of *B. praecursor*, s.l. It is transitional between *B. praecursor* var. *media*, n. var., and the representative of *B. praecursor* var. *mucronatiformis* n. var. reproduced on Pl. 58, figs. 2a–b.

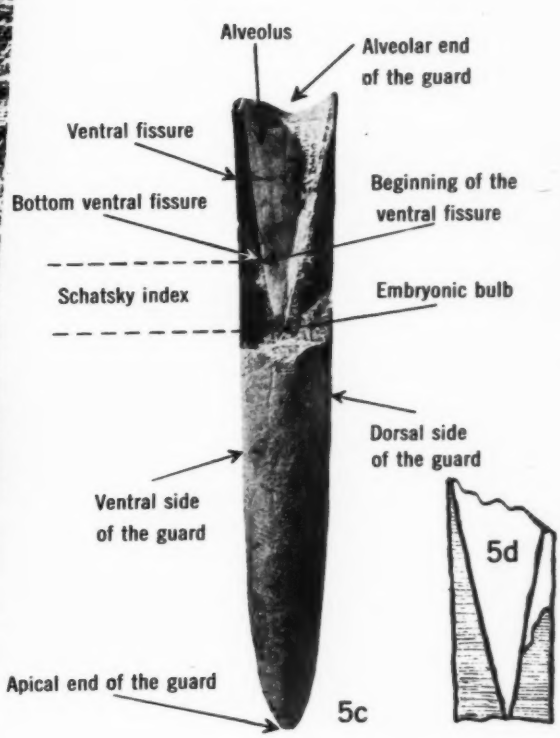
The relatively strong development of the transverse to oblique vascular imprints and of the longitudinal markings and striae over most of the guard, combined with its acute and essentially nonmucronated apical end, are characteristic of this variety. The relatively long ventral fissure and its shortened, slightly and irregularly bent bottom, forming a greater angle with the wall of the alveolus than in the other varieties of *B. praecursor*, s.l. (compare figs. 1–3), and the still evident predominance of the longitudinal markings and striae over the vascular imprints, are equally characteristic of this variety. The outline of the bottom of the ventral fissure is typical of *B. praecursor* var. *mucronatiformis*, n. var. It is strongly reminiscent both of that of the slender varieties of *B. mucronata* (Schlotheim) n. var., of the upper Campanian and of that of *B.* ex gr. *B. mirabilis* Arkhangelsky of the older Santonian. Exactly the same outlines of the ventral fissure occur in the Russian representatives *B. praecursor* var. *mucronatiformis*, n. var., in the local zone of *Pteria tenuicostata* Roemer.

Such forms are very rare in the zone of *Diplacmoceras bidorsatum* and in the lower part of the *Pteria tenuicostata* zone but become rather common in the upper part of the latter zone. (p. 497)









Jeletzky, *Belemnitella praecursor* Stolley

given by studies of McLearn (1951) Haas (1946), Kaufmann (1933), Jayet (1929), Wepfer (1911, 1913), Woods (1912), Rowe (1899) and Stolley (1897, 1911). Such attempts, which in the opinion of the writer are highly laudable, go back to the old master of "ammonitology," F. A. Quenstedt (1849, 1858, 1883–1888), whose natural and comprehensive species subdivided into numerous morphological varieties present a far better solution of the taxonomical problems in paleontology than the ultrafine morphological species of modern authors. A partial return to Quenstedt's taxonomic principles might well be the best solution of many difficulties in modern taxonomy and nomenclature. As pointed out by Holder (1952, pp. 272–273), this old master has tried, at least subconsciously but rather successfully, to define taxonomically evolutionary streams of forms rather than to describe rigid, and static, morphological types. This has put him far ahead of his contemporaries and even ahead of a great many of today's paleontologists.

The fact that paleontological varieties and species, as defined above, differ strongly from the corresponding neontological taxonomic categories in spite of their many features in common, appears quite natural to the writer. It is basically the ever-present and all important dimension of geological time in paleontology and its virtual nonexistence in neontology that opposes essentially static and morphological neontological classifications to thoroughly historical and dynamic paleontological ones. This important distinction and its far-reaching implications, unfortunately insufficiently appreciated, were stressed by Borissiak (1928, p. 131; 1947, p. 68), Elias (1949, p. 148–149; 1950, p. 176–177), Tripp (1950, p. 92), and Jeletzky (1949a, p. 268; 1950a, p. 25) and Bell (1950). Arkell (1950), Schindewolf (1950b), Simpson (1951, pp. 290–297), Wright (1952, p. 213), and McKerrow (1952), though arguing for the retention of the neozoological classification in paleozoology, have at least partly recognized this distinction.

The writer believes that any paleontological classification should be dynamic and phylogenetical at all levels down to specific and subspecific categories. The concepts of time and derivation must, indeed, be brought in to define all its categories, and not only the higher ones, as Wright (1952, p. 213) has recently suggested. As clearly perceived already by Rowe (1899, p. 495–498, 541–543), the taxonomic value of any morphological character in paleontology can only be correctly appraised when its phylogeny and relative grade of stability in time and in space become sufficiently understood.[1]

Another difficulty in dealing with short-lived and reversible morphological shifts lies in the possibility of connecting them into imaginary parallel evolutionary trends, particularly when the fossil material is

[1] The manuscript was completed and sent off to the publisher prior to the appearance of the latest works of G. G. Simpson in which some of the problems of paleontological systematics dealt with in the preceding pages are discussed at some length [(1) Life of the Past; An Introduction to Paleontology, Yale University Press, 1953, pp. 93–106, table 2; and (2) The Major Features of Evolution, Columbia University Press, 1953, pp. 386–388, fig. 51]. One point of the procedure in paleontological systematics adopted by Simpson in these works should, however, be discussed here. His paleontological species are equivalent to the vertical genera of Simpson (1945) and of this paper. Similarly, Simpson's subspecific chronological stages of a paleontological species correspond to the specific chronological stages of this paper. From a purely paleobiological standpoint Simpson's approach may well be advantageous in stressing the phylogenetical continuity of a given lineage (plexus), which is less apparent if its subsequent chronological stages are treated as independent paleontological (=chronological) species. The latter approach adopted in this paper has, however, the advantage of recognizing the practical needs of the stratigraphical paleontologists and the current practice of paleontologists. Chronological subspecies (or Waagen's mutations) are, indeed, but seldom used in paleontological literature where morphologically distinctive, allied forms occurring at different stratigraphical levels are nearly always treated as species or genera (horizontal genera). The terms variety and subspecies are, on the contrary, almost exclusively used by paleontologists for various kinds of closely allied, morphologically distinctive but geologically contemporary forms. An attempt to reverse this time honoured practice for reasons quite irrelevant for stratigraphical paleontologists and comparatively unimportant for paleobiologists themselves is not likely to be generally acceptable. Furthermore, it has been pointed out in the earlier pages of this paper that the concurrent use of chronological subspecies, geographical subspecies, and varieties within each paleontological species is inconvenient in needlessly overburdening the nomenclature.

scarce, poorly preserved or stratigraphically unreliable. As already pointed out, were it not for the large and accurately located collections of *Belemnitella* forms from the lower and upper Campanian substages in the Dniepr-Donetz depression, the writer might easily assume the presence of an independent phylogenetical trend connecting *B. praecursor* Stolley, s.l., with *B. mucronata* (Schlotheim) mut. *senior* Nowak, closely paralleling that of the minor mucronated forms. The writer suspects strongly that some of the parallel evolutionary trends of Devonian goniatites and *Clymenia* postulated by Schindewolf (1928, pp. 128–162; 1936, p. 40, fig. 25; 1950a–b) might at least be partly illusory and of the same plexus. The same might easily be the case with the allegedly independent and parallel trends connecting several species of *Quenstedtoceras* directly with individual species of *Cardioceras*, postulated by Smorodina (1926) and accepted as valid by Spath (1932, pp. 48–49)and Arkell and Moy-Thomas (1940, pp. 398–399). Many more examples could be easily cited.

CONTINUOUS EVOLUTION AND CRYPTOGENIC FORMS

Since the time of general acceptance of the theory of evolution, it has been recognized by all Darwinists, whether neontologists or paleontologists, that an entirely gradual transition between species, genera and higher taxonomic units is the rule for all groups of fossils. Rowe (1899) and Stolley (1911, pp. 7–10), for example, have emphatically stressed the validity of this Darwinian principle, as applied to Upper Cretaceous echinoids, belemnites, and to invertebrate fossils in general. Simpson (1944, 1945) has done the same for vertebrates.

The general statement that most or all sharp morphological boundaries between allied paleontological species and genera are either the result of the incompleteness of the geological record or, more often, the result of the failure of paleontologists to pay sufficient attention to intermediate forms, is, however, in need of a few qualifications. There are, indeed, a great many cases in which the sharp, morphological boundaries between paleontological species and genera really do occur at a given locality or over larger areas and regions. Neumayr (1878, pp. 37–80) has shown that a great number of species of Jurassic ammonites appear and disappear suddenly and have neither known ancestry nor descendants. Such forms are called "cryptogenic forms." This well known fact at first appears to be contradictory to, and is used as an argument against, the Darwinian interpretation of evolutionary changes by Salfeld (1913, pp. 437–440; 1921, pp. 46–59, 1922), Schindewolf (1928, 1936, 1947, 1950a–b) and by a great many other authors. However, there is no real contradiction at all. Darwin himself recognized in the "Origin of Species" that every evolutionary development takes place only within a more or less limited area or region. Even for marine animals, such areas often do not exceed the limits of one sea basin. Under such circumstances, around the areas or regions of evolutionary development of any fossil group there is bound to be a belt, or several isolated irregular areas or regions, into which only certain of its evolutionary stages would penetrate. There, these "fragments" of the elsewhere complete evolutionary record of the group are bound to be completely isolated, sharply defined, "cryptogenic forms" as long as their evolutionary area remains unknown. Salfeld (1924) himself has shown that the "cryptogenic forms" of the mid-European Jurassic ammonite faunas are most probably consecutive waves of immigrants from the Mediterranian geosynclinal sea, where they originated in the so-called conservative stocks Lytoceratida and Phylloceratida. Spath (1923–43, p. 14) expressed the same idea in 1923 in advancing the theory of: "the repeated replenishment of the ammonite tribe from the radical *Phylloceras-Lytoceras* stock." Thus, the common occurrence of sharply defined species that do not integrade with their nearest allies above and below, cannot, if taken by itself, be interpreted as an argument in favour of evolution by abrupt, jump-like genotypical changes from one morphological form to another, as it was thought by the above mentioned authors, and by a great many other paleontologists. Rensch (1929, pp. 118–127, 172–184; 1947, pp. 14–19, 104 ff.) and Kaufmann (1933, p. 18) were apparently the first modern authors to expose the general inadequacy of the above interpretation of

paleontological mutations and the advantages of the zoogeographical explanation of sudden appearances of new species in the geological past. In the Belemnitellidae the writer has so far never met with any "macroevolutionary" morphological changes that would be contradictory to the neo-Darwinian concept of gradual, "micro-evolutionary" transmutation of extinct organisms. Accordingly, at least on specific and generic levels, he does not see any necessity for such an explanation of evolutionary gaps, which are so common in paleontology. He would assume that all known cryptogenic and morphologically sharply limited species and genera are known only from areas or regions lying outside of their evolutionary areas. For instance, forms like *B. mucronata* (Schlotheim) mut. *anterior* of Stolley (1897) (?=*B.* ex gr. *B. mirabilis* Arkhangelsky), *B. praecursor* Stolley, and *A. lundgreni* Stolley were bound to remain more or less enigmatic in northwestern Europe and England both in their genetic relationships and stratigraphical ranges until their respective places within the plexus of late *Actinocamax* and early *Belemnitella* forms were recognized in European Russia (Jeletzky, 1948b, pp. 593–595; 1950a, p. 33, text-fig. 2; early pages of this paper). On the other hand, genetic relationships, valid morphological distinctions, and the stratigraphical ranges of *Actinocamax westfalicus* and of *Gonioteuthis granulata—G. quadrata* could only be understood in northwestern Europe, where the area of the evolutionary development of this group was situated (Jeletzky, 1948b, pp. 593–595; 1950a, p. 33, text-fig. 2) and all stages of their plexus are preserved. This was actually done by Stolley (1897, 1916, 1930), whose conclusions are still valid even in details.

It should be quite evident that local conditions in England and in northwestern Europe should under no circumstances be interpreted as contradictory to the plexus relationships of *B. praecursor*, s.l., and its ancestors in European Russia. The same is true with regard to isolated records of *Gonioteuthis* ex gr. *G. granulata—G. quadrata* in European Russia, Mangyshlak, Caucasus, etc., as compared with the plexus relationship of the same forms in northwestern Germany.

The above conclusions notwithstanding, the present writer does not reject the "macroevolutional" concept outright. It is still adhered to by such outstanding specialists as Schindewolf (1928, 1936, 1947, 1950a–b), Goldschmidt (1952), and Petrunkevich (1952). Moreover, it seems to find support in fundamental morphological and evolutionary studies of Sewertzoff (1912, 1925, 1931, 1939, pp. 510–519, 590), who has introduced the term "archallaxis" for such abrupt and morphologically pronounced changes observed at the very early stages of ontogeny. Thus the "macroevolutionary" modus yet might be found to be valid, at least in some rare and exceptional instances (Simpson, 1945, p. 17).

SYSTEMATIC DESCRIPTIONS

Genus BELEMNITELLA d'Orbigny, 1842, emend. Jeletzky, 1941

Type species: *Belemnites mucronatus* Schlotheim, 1813

BELEMNITELLA PRAECURSOR Stolley, 1897, s.l.

Pl. 56, figs. 1–5; Pl. 57, figs. 2–4; Pl. 58, figs. 1–2, 4

Belemnitella lanceolata BLACKMORE, 1896, pp. 529–530, pl. 16, fig. 1.

Belemnitella praecursor STOLLEY, 1897, pp. 297–299, pl. 3, fig. 24.——GROSSOUVRE, 1899, p. 134.

Belemnitella lanceolata ROWE, 1900, pp. 345–346 (from the *quadrata* chalk only).——ROWE, 1902, p. 61 (from the *quadrata* chalk only).——JUKES-BROWNE, 1904, pp. 11, 65 (from the *quadrata* chalk only), 81, 84, ?122–123, 246–247, 265 (from the *quadrata* chalk only).

Belemnitella praecursor STOLLEY, 1906, pp. 92–93.——MÜLLER & WOLLEMANN, 1906, p. 29, pl. 6, figs. 7–8.——GROSSOUVRE, 1908, p. 406.

Belemnitella lanceolata ROWE, 1908, pp. 314–315.——CRICK, 1910, p. 365 (footnote).

Belemnitella mucronata SPULSKI (in Törnquist), 1910, p. 60 (only the *B. mucronata* forms associated with *Actinocamax* sp. in the lower Senonian of eastern Prussia).

Belemnitella lanceolata BRYDONE, 1912, p. 100.

Belemnitella praecursor ARKHANGELSKY, 1912, pl. 9, figs. 1–2, 8, 22; pl. 10, fig. 33.

Belemnitella lanceolata RAVN et al., 1913, pp. 100–101.

Belemnitella praecursor SINTSOV, 1915, p. 158, pl. 8, fig. 13 a–b.

Belemnitella of the typus *B. praecursor* DENISOVA & KRESTOVNIKOV, 1924, p. 63.

Belemnitella praecursor SCHATSKY, 1924, pp. 92–95, 116, 121–123.——KRESTOVNIKOV, 1924, p. 192.——KAHRS, 1927, p. 683.

Belemnitella lanceolata BRYDONE, 1933, pp. 286, 290.

Belemnitella praecursor VASILEVSKY & ARKHANGELSKY, 1934, p. 47 (including the intermediate forms between *B. praecursor* and *B. mucronata* mentioned herewith).

Belemnitella lanceolata LUNDEGRENA, 1934, pp. 300–301.

?*Belemnitella* of the typus *B. praecursor* DUBIANSKY, 1935, pp. 46–47.

Belemnitella praecursor BESRUKOW, 1936, p. 104.

Belemnitella of the typus *praecursor* JELETZKY (Eletsky), 1940, pp. 125–128.

Belemnitella praecursor JELETZKY, 1941, pp. 23, 28.

?*Belemnitella lanceolata* WRIGHT & WRIGHT, 1942, p. 20.

Belemnitella lanceolata HÄGG, 1947, pp. 98–99 (the specimen from the Danish boring Gröndals Eng only).

Belemnitella ex gr. *B. praecursor* JELETZKY, 1948b, pp. 593–594, and the correlation table.

Belemnitella praecursor JELETZKY, 1948c, p. 344, figs. 5–6 (only the specimens of Blackmore, not those of Sharpe and Jukes-Browne).—— VASSILENKO & RASMYSLOVA, 1950, pp. 605–606, text-fig. 1a.——WRIGHT & WRIGHT, 1951, p. 10.——JELETZKY, 1951b, pp. 83–85, pl. 1, figs. 1–2.

Historical review

The existing confusion about *Belemnitella praecursor* Stolley is mainly due to excessive reliance upon the taxonomic importance of certain external morphological characters of the guard of *Belemnitella*-like forms, fully discussed by Jeletzky (1949a, pp. 257–262).

Even before the naming of *B. praecursor* by Stolley (1897), *Belemnitella* forms conspecific with it were recorded and even figured (see Blackmore, 1896, pl. 16, fig. 1) from the lower part of the *quadrata* zone of England. These, however, were always erroneously identified as *Belemnites lanceolatus* Schlotheim, 1813. This identification of *B. praecursor* with the homeomorph *Belemnella lanceolata* (Schlotheim), characteristic of English authors, was discussed by Jeletzky (1948c, pp. 343–346; 1949a, pp. 262–266; 1951a, pp. 204–205).

These records of *Belemnitella* conspecific with *B. praecursor* remained unknown to Stolley (1897), and British authors also appear to have been unaware of his publication of *B. praecursor*, perhaps due to the fact that Stolley's paper was published in a local German periodical.

It should be stressed that all English authors have understood *B. praecursor* in a broader sense than Stolley did, while at the same time insisting on its intergrading and close affinity with *B. mucronata* (Schlotheim). Already in 1902 Rowe (1902, p. 61) was aware of that. At that time, however, he wrongly assumed that "*B. lanceolata*" (=*B. praecursor*) occurs in both the *quadrata* and *mucronata* chalk of England. Later, after having given up his views as to the occurrence of "*B. lanceolata*" (=*B. praecursor*) in rocks younger than the *quadrata* zone, and having stressed its restriction to this zone, Rowe (1908, pp. 314–315) fully confirmed his earlier conclusion about the intergradation and close affinity of "*B. lanceolata* (=*B. praecursor*) with the younger *B. mucronata*.

Crick (1910, p. 365, footnote), who rightly stressed that *B. lanceolata* of Sharpe (1853–57) and of Jukes-Browne (1904, p. 12) is not the same form as *B. lanceolata* of Blackmore (1896), and Brydone (1935, p. 286), fully confirmed the conclusion of Rowe as to the intergradation and close affinity of *B. lanceolata* of Blackmore (=*B. praecursor*) with *B. mucronata* s.l.

Arkhangelsky (1912) showed that *B. praecursor* Stolley occurs abundantly, or at any rate commonly, in his zones of *Inoceramus pachtii* and *Pteria tenuicostata* all over European Russia and the northwestern parts of Russian middle Asia (Emba region, northern Kasakstan, etc.). Arkhangelsky (1912, p. 606) was also able to show that the more or less typical *B. praecursor* of his paleontological zones is connected by all possible intermediate forms with the typical *B. mucronata* [mainly *B. mucronata* (Schlotheim), mut. *senior* Nowak, in the sense of the present writer] from the immediately overlying zone of *B. mucronata*. Both forms, however, were retained as separate species since they were found by Arkhangelsky (1912, p. 606) not normally occurring together and characteristic of two successive paleontological zones. It is remarkable that the study of the Russian *B. praecursor* by Arkhangelsky (1912) and later authors led them to a concept of this species rather different from that of Stolley (1897) but very close to that developed earlier by Rowe (1902, 1908), Blackmore (1896), and Crick (1910).

Arkhangelsky (1912) was the first to rec-

ognize the specific identity of the early Russian "*mucronata*" forms with *B. praecursor* Stolley and with "*B. lanceolata*" of Blackmore, he also proved the specific distinction between this latter and *Belemnites lanceolatus* of Schlotheim (1813). Arkhangelsky (1912, p. 604) and, following him, Jeletzky (1948c, pp. 343–346; 1949a, p. 264) have, however, overlooked the fact that more than one *Belemnitella*-like form superficially similar to *B. praecursor* Stolley was recorded, described, and figured in England under the name *Belemnites lanceolatus* Sharpe, 1853–57, non Schlotheim, 1813. At the present time it seems to be sufficiently apparent that, whatever the real nature of *Belemnites lanceolatus* Sharpe (1853–57) non Schlotheim (1813) may be, it is not the same as *Belemnitella lanceolata* Blackmore, 1896, non Schlotheim, 1813 (see also Crick, 1910, p. 365, footnote; Wright and Wright, 1951, p. 10; Jeletzky 1951a, pp. 204–205), which is specifically identical with *B. praecursor* Stolley.

In England no attempt appears to have been made to inquire further into the taxonomic position, morphological characters, and stratigraphical range of "*B. lanceolata*" of Blackmore (1896) after the appearance of Brydone's (1933) paper. Brydone (1933, pp. 286–287) was, however, fully aware of the still unsatisfactory state of knowledge of this and other British Upper Cretaceous belemnites and of a "crying need . . . for a thorough study of the belemnites of the Upper Chalk."

The allusions to *B. praecursor* Stolley made previously by the writer are listed under its synonymy in this paper and his views, together with the necessary additions and adjustments, are discussed below. His conclusions regarding the distinction between *Belemnitella lanceolata* of Blackmore and *Belemnella lanceolata* of Schlotheim on specific and generic levels were recently accepted as valid by Wright and Wright (1951, p. 10) in England. The perennial confusion of both these forms in that country was thus put to an end.

Concept of species

B. praecursor, s.l., represents an evolutionary stage of the *Belemnitella* plexus, which merges imperceptibly into the preceding and succeeding evolutionary stages of the same (see above, Text-fig. 1). Moreover, a certain number of specimens indistinguishable from this species are known to occur somewhat below its proper range, to ascend into the younger beds characterized by *B. mucronata* (Schlotheim), s.l., and so to mingle with ancestors or descendants of *B. praecursor*. In spite of this it is quite possible to characterize our species morphologically and to use it stratigraphically, as its total time range is very long as compared with zones of intergradation (transmutation) below and above. These latter are clearly defined for all practical purposes, for the transmutation of *B. praecursor* Stolley, s.l., occurs very rapidly, geologically speaking (see part of this paper on stratigraphic range).

The great majority of *Belemnitella* guards within the total time range of *B. praecursor* can be easily recognized and referred to the intermediate ("mean") form of the species, its extreme morphological varieties, or to some kind of passage forms between them. They are all distinct morphologically from any known *Belemnitella* form from older or younger beds, not excluding such "recurrent" forms as *B. lanceolatus* Sharpe non Schlotheim. Even the extreme, *B. mucronata*-like variety, *B. p.* var. *mucronatiformis*, n. var., occurring throughout the time range of the species, can be easily distinguished morphologically from *B. mucronata*-like forms from the older and younger beds, for it closely approaches the average forms of the species in most morphological characters.

It should be strongly emphasized that the morphological differentiation of *B. praecursor* Stolley, s.l., from its ancestors and descendants is possible only if it is remembered that all the diagnostic morphological characters used represent a certain generalization and "typification," which can rigidly apply only to a certain number of more or less "typical" specimens among the endless variety of morphological forms comprising this species. All forms connecting *B. praecursor* Stolley var. *media*, n. var., with its ancestors and descendants, and with the accompanying *B. p.* var. *praecursor* Jeletzky and *B. p.* var. *mucronatiformis*, n. var., can, and should, be designated only as intermedi-

ate forms. No attempt should be made to fit them rigidly into the more abstract morphological concept of the species or its morphological varieties. Such attempts are neither necessary nor desirable, as the presence or absence of certain intermediate or extreme morphological forms in addition to more or less "typical" ones in the given sample of a paleontological population represents one of the most valuable means of recognition of the precise stratigraphic position of the given bed or even layer within the succession characterized by the given species as a whole. This fact, though clearly recognized by some outstanding paleontologists decades ago (e.g. Rowe, 1899, pp. 495–498, 541–543; Stolley, 1911, pp. 7–10; 1916, pp. 95–104) and successfully used by many more investigators the world over, is still far from being generally recognized by the rank and file of paleontologists (see Jeletzky, 1950a, pp. 25–29 and later pages of this paper).

The above approach to the delimitation of *B. praecursor*, which certainly greatly facilitates its consequent application, was advanced by Rowe (1902, 1908) in England and by Arkhangelsky (1912) in Russia. Jeletzky (1951b, pp. 80–81) has applied the same approach to the immediate descendant of *B. praecursor*, viz. *Belemnitella mucronata*, s.l., and to some other *Belemnitella*-like forms.

Type specimen

The guard figured by Stolley (1897, pl. 3, fig. 24) is the holotype of the species *Belemnitella praecursor*. It appears to have been misplaced or lost since its description, as the present writer did not find it in the collections of the University of Kiel, Schleswig-Holstein, Germany, where it was said by Stolley (1897, p. 302, expl. of plates) to be deposited. The figures of Stolley (1897) are, however, good and quite sufficient for the recognition of the diagnostic features of the holotype without reference to the specimen.

Material studied

The revision of *B. praecursor* Stolley attempted here is based on some 200 specimens personally collected bed by bed on the northeastern slope of the Dniepr-Donetz depression and on the northwestern border of the Donetz basin. The former region has supplied the bulk of these collections and all the transitional forms to the ancestors of *B. praecursor* discussed above. On the northwestern border of Donetz basin the beds underlying those with the typical *B. praecursor* are barren of any *Belemnitella* forms.

In addition, several scores of well preserved specimens of *B. praecursor* were studied in the museums of Moscow and Leningrad. These cover nearly the whole paleogeographical range of this species in European Russia described below and fully support the conclusions derived from the study of personal collections of the writer.

Eight specimens of *B. praecursor* from England were also studied, together with a few guards from Lithuania, eastern and western Prussia, and Scania; these are listed below in connection with the discussion of the paleogeographical range of *B. praecursor*.

Morphology

By way of explanation of the various technical terms used below in the description of the guard of *B. praecursor*, s.l., most of its important morphological features are indicated on Pl. 56, figs. 5a–c.

The guard is long, normally more or less slender, moderately stout forms occurring rarely. In ventral aspect it is mostly slightly to moderately lanceolate, with a slight contraction nearly always present at about one quarter of the total length of the guard from the alveolar rim. Pronouncedly lanceolate guards, or ones gradually tapering from the alveolar rim to the apical end, or ones cylindrical in ventral aspect are rare. In lateral aspect, the guard is always slightly to moderately conical; tapering occurs very gradually all the way down to the very apical end. The same, very gradual, tapering occurs also in ventral and dorsal aspects, below the alveolar contraction mentioned above. This tapering results in a long, acute apical end of the guard, which totally or nearly lacks a distinctly separated mucro and rounded obtuse base. Both these features are much less characteristic of the late forms of the species or of such transitional to *B. mucronata* (see Pl. 58, figs. 1a–c, 2a–b).

In the adult state, the length of the guard usually averages from 100 to 130 mm. The average maximum widths in dorso-ventral and lateral directions are apparent from Pls. 56–58. About half the guards studied are nearly circular in cross section all the way from the alveolar rim to the apical point, (see Pl. 57, figs. 2a–b). A more or less pronounced flattening of the ventral surface is fairly common (see Pl. 57, figs. 3a–b; Pl. 58, fig. 2a–b), and there are many intermediate specimens between both extremes. In markedly flattened specimens the lateral diameter exceeds the dorso-ventral, except in the alveolar third of the guard where the values of the dorso-ventral diameter are always greater than those of the lateral. Flattening of the dorsal side of the guard is rare but by no means unknown. The more or less markedly developed dorso-lateral, longitudinal depressions result in a protrusion of the median zone of the dorsal side of the guard. This protruding and somewhat ridge-like zone becomes narrower, and at the same time more elevated, towards the alveolar rim. It is practically absent on the apical half of the guard.

The surface of the guard is usually only feebly sculptured with some slight, somewhat irregular, longitudinal markings and striae, and a few rather weak vascular imprints. The longitudinal markings are usually dominant with respect to the oblique or transverse vascular imprints. The surface of the guard around the ventral fissure is nearly always smooth or carries only a few weak longitudinal markings. A dense fine mesh of the vascular markings was never observed. The surface of the guard may, however, be quite smooth, as for example in the specimens figured by Müller and Wollemann (1906, pl. 6, figs. 7–8) or in the holotype of the species figured by Stolley (1897, pl. 3, fig. 24). Another extreme is represented by some comparatively strongly sculptured specimens, otherwise indistinguishable from the "mean" representatives of the species, (see Pl. 58, figs. 1a–c, 2a–b; Pl. 56, figs. 5a–d). Even these latter forms are never as strongly sculptured as a typical *B. mucronata* (Schlotheim).

Dorso-lateral double furrows and the longitudinal depressions harbouring them over the upper two-thirds of the flanks of the guard are usually distinctly developed. They are however, always more feebly developed than those of *B. mucronata*. Their character, and that of the main branches of the vascular imprints branching off them in the lower third of the guard, are in no way different from those of *B. mucronata* or of the other *Belemnitella* species, except that the main vascular branches are also always quite feeble and few in number. They may be absent altogether, as already mentioned.

The ventral fissure is relatively short. Even in almost complete guards, such as those figured on Pl. 57, fig. 2, 4, it does not exceed 25 mm. in length. Normally its length fluctuates between 10 and 20 mm. so that it does not descend below the upper third of the alveolus. The alveolus is wide, conical, almost circular in cross section, though it may be also somewhat oval in the earlier representatives of the species. The conotheca is white or whitish-grey, always less than 1.0 mm. in thickness. To the naked eye it appears to be quite smooth in most instances, with the exception of a small area near the apex of the alveolus. Within this latter area the surface of the conotheca is completely covered with a fine, shagreen-like ornamentation, which usually reaches a line from 10 to 30 mm. above the embryonic bulb. A strong pocket lens or a binocular shows that this ornamentation consists of tiny, rounded but irregularly-shaped tubercles and pits. These reach maximum dimensions in the lower 3 to 6 mm. of the aforementioned area. In the higher parts of the alveolus these tubercles and pits quickly decrease in size and mostly become invisible to the naked eye within a few millimeters. A strong pocket lens or a binocular shows that they extend further, for a variable distance, toward the alveolar rim—sometimes all the way up to it. In a relatively few specimens the surface of the conotheca is covered with the tubercles and pits discernible to the naked eye to the very alveolar rim, but even in such cases the coarser tubercles and pits, clearly visible to the naked eye, are restricted to a small area immediately above the embryonic bulb. The typical development of this ornamentation of the conotheca is shown on Pl. 56, fig. 4.

The surface of the conotheca sometimes

shows the imprints of the chambers of the phragmacone (see Pl. 57, fig. 2c). The phragmacone was never preserved in our material. The depth of the alveolus averages, as a rule, between a third and two-fifths of the total length of the guard in the best preserved specimens available. Sometimes it approaches closely to one-half of the total length of the guard, but is not known to reach this figure even when the guards are almost complete. The alveolar angle, measured in the dorso-ventral plane, averages 20–22 degrees in our material, this value appears to be very constant and figures below 19 degrees are unknown to the writer. In almost all cases the bottom of the ventral fissure forms a straight or nearly straight line, running very close to the inner wall of the alveolus so that the angle between the two does not usually exceed 5–10 degrees (see Pl. 57, fig. 2c; Pl. 58, fig. 1c; Pl. 56, fig. 2). Figures in excess of 15–20 degrees are unknown to the writer, as far as the typical specimens are concerned. In every large suite of the specimens of our species there are, however, a few (probably between 0.5 to 2.0 percent of the total) guards which are somewhat anomalous in this respect. The extremes are shown on Pl. 56, figs. 1, 3, 5c–d. The beginning of the ventral fissure on the inner side of the alveolus (so-called Schatsky index; see Jeletzky, 1949a, p. 259, foot-note) is always situated from 6–10 mm. above the top of the embryonic bulb, which occupies the apex of the alveolus. The average figure for this important morphological feature is 7–8 mm. The embryonic bulb is usually somewhat displaced toward the ventral side of the guard, the average amount of displacement being about two-fifths of the total width of the guard. Also the axial line of the guard is somewhat displaced toward the ventral side of the latter. It only begins to swing gradually back toward the median position in its apical quarter, the apical point being either central or slightly displaced toward the dorsal side of the guard.

Ontogeny

The earliest observable juvenile guards of *B. praecursor* Stolley are very slender and markedly lanceolate in ventral aspect. They taper gradually laterally and have a rather acute apical end. Later, but still juvenile, guards retain the same character and very much resemble those of the adult *Actinocamax lundgreni* Stolley or of adult slender variants of *Belemnitella propinqua* (Moberg). Even the semi-adult guards of *B. praecursor* retain almost the same form of the guard except that they gradually become somewhat stouter and not quite as acutely pointed as the younger ones. Study of all the growth stages of the species in the collections from the zone of *Inoceramus* ex gr. *I. cardissoides* of the Dniepr-Donetz depression (see Jeletzky, 1948b, p. 593–595, Beilage 1; 1951b, pp. 83–85) has given exactly the same results as the study of the growth lines of the adult guards in the dorso-ventral polished plates. A typical ontogeny of *B. praecursor* is reproduced by Jeletzky (1948c, p. 344, text-fig. 5b; 1951b, pl. 1, fig. 2a).

Affinities and differences

B. praecursor, s.l., is characterized by a weak to absent sculpture of the surface of the guard, by predominance of weak, longitudinal, somewhat irregular striae and markings over the oblique or transversive, branching vascular imprints in the sculptured specimens, and by completely or nearly smooth surface of the guard all around the alveolar fissure. The guard is generally slender, high, and long, tapering gently laterally, subcylindrical to sublanceolate in ventral aspect; its rather gradual tapering in the apical direction results in an acute apical point, without or nearly without the obtuse, mucronate base so characteristic of its descendants, beginning with *B. mucronata*, s.l. In combination with the shorter ventral fissure and the shallower alveolar cavity, which carries at least a certain amount of ornamentation, the above morphological features are ample for a safe distinction of *B. praecursor*, s.l., from all its upper Campanian and Maestrichtian descendants.

B. praecursor, s.l., is easily differentiated from its predecessors, such as *Belemnitella propinqua* (Moberg), *B.* ex gr. *B. mirabilis* Arkhangelsky, *B.*, n. sp., aff. *B. praecursor* Stolley (including *B.* ex aff. *B. mucronata* Schlotheim), by its straight to nearly straight, long bottom of ventral fissure,

much deeper alveolus (except in *B.*, n. sp., aff. *B. praecursor*), absence or lesser amount of dorso-ventral flattening of the guard, less marked vascular imprints and longitudinal markings, and lesser development of the obtuse, mucronated apical end of the guard. The almost smooth (for the naked eye), thin, always preserved conotheca, with the visible coarser ornamentation nearly always restricted to a narrow apical zone of the alveolus, presents perhaps the best individual feature of *B. praecursor*, s.l., distinguishing it from its predecessors. These predecessors, with the exception of *B.*, n. sp., aff. *B. praecursor*, and the intermediate forms between this and *B.* ex gr. *B. praecursor-mucronata*, all possess much thicker and coarsely sculptured conotheca with the coarsest tubercles and pits near the rim of the alveolus (see Jeletzky 1949b, pp. 415–418; early pages of this paper).

The differentiation of *B. praecursor* from such "recurrent," weakly sculptured, and acutely pointed forms of the upper Campanian and Maestrichtian as *B. lanceolatus* Sharpe, 1853–57, non Schlotheim, 1813, or superficially similar forms of *B. americana* (Morton, 1830) non Arkhangelsky, 1912, deserves some special consideration. *B. lanceolatus* Sharpe non Schlotheim is distinguished by its relatively shorter guard and much longer ventral fissure. The rarely encountered, hitherto undescribed, weakly sculptured and acutely pointed forms of *B.* ex gr. *B. americana*, are even longer than *B. praecursor*, but the irregular outline of the bottom of the ventral fissure and its very great length always enable one to differentiate the two.

A detailed discussion of affinities and differences between *B. praecursor*, s.l., and the Eurasian upper Campanian and Maestrichtian *Belemnitella* species was given by Jeletzky (1951b, pp. 83–105).

Morphological varieties and chronological infraspecific forms

The completely smooth guards of *B. praecursor* described and figured by Stolley (1897) and Müller and Wollemann (1906) have been shown in this paper to represent only an extreme morphological variety of this polytypic species. This variety was named *B. praecursor* var. *praecursor* by Jeletzky (1951b, p. 85). Morphological descriptions and illustrations of *B. praecursor* by Stolley (1897) and by Müller and Wollemann (1906) apply to this variety alone. The specimen figured by Stolley (1897, pl. 3, fig. 24) was designated as holotype of *B. praecursor* var. *praecursor* by Jeletzky, (1951b, p. 85).

The more common and morphologically intermediate form of the species may be conveniently named *B. praecursor* var. *media*, n. var., and the guard reproduced on Pl. 57, fig. 4a–b, Pl. 56, fig. 2 designated as its holotype. This variety is characterized by the presence of numerous, faint, longitudinal striae on both the ventral and the dorsal surfaces of the guard, which may also be present on its sides. Double dorso-lateral furrows and single lateral furrows are also present, accompanied by at least a few, weak vascular imprints, in most specimens. The guards figured by Arkhangelsky (1912, pl. 9, 1–2, 8, 22; pl. 10, fig. 33) and Sintsov (1915, pl. 8, fig. 13a–b), and the drawings of *B. praecursor* given by Jeletzky (1948c, text-figs. 5a–b, 6; 1951b, pl. 1, fig. 1, 2a–b) represent this variety.

Since the study of Arkhangelsky (1912), almost every Russian student (e.g. Denisova and Krestovnikov, 1924, p. 63; Vasilevsky and Arkhangelsky, 1934, p. 47) has stressed the presence of feebly sculptured forms referable to *B.p.* var. *media*, n. var., together with the extreme, smooth forms belonging to *B. praecursor* var. *praecursor*. In northern and northwestern Europe and in England such forms were probably referred either to *B. mucronata* or to "*B. lanceolatus*."

In addition to its designated holotype, the guards reproduced on Pl. 57, fig. 2a–c, fig. 3a–b; Pl. 58, fig. 4a–b; Pl. 56, figs. 1, 3 represent *B.p.* var. *media*, n. var.

Another extreme morphological variety of *B. praecursor*, s.l., is represented by forms fairly strongly sculptured with longitudinal striae and vascular imprints over most or all the surface of the guard, and more or less pronouncedly mucronated. They are mostly slender and somewhat lanceolate in ventral aspect. The writer names them *B. praecursor* var. *mucronatiformis*, n. var., in order to stress the persistence of *B. mucronata*-like morphological forms through the zone of *B. praecursor*, s.l. The guard reproduced on

Pl. 56, fig. 5a–d is designated as the holotype of *B.p.* var. *mucronatiformis*, n. var. It represents the typical, smaller lanceolate form of this variety, somewhat approaching in this respect *B. praecursor* var. *media*, n. var. Its larger and more mucronated representative reproduced on Pl. 58, fig. 2a–b is less typical and transitional to the slender varieties of *B. mucronata* (Schlotheim).

With regard to the distinction of "high" and "low" forms of the species, as shown on Text-fig. 1, it appears in general that smooth, or nearly smooth, forms with a very short ventral fissure, more strongly developed ornamentation of conotheca, very long and straight bottom of ventral fissure, shallower alveolus and acutely pointed, non-mucronated apical end are characteristic of the lower half of the stratigraphical range of *B. praecursor* Stolley, s.l. The extreme variety *B. praecursor* var. *praecursor* Jeletzky, 1951, in the present state of our knowledge, is nearly restricted to the uppermost Santonian and to the zone of *Diplacmoceras bidorsatum* (Roemer). The writer has only seldom encountered it in the upper part of the lower Campanian. Forms with smooth or nearly smooth surface of the guard around the ventral fissure are also indicators of the lower half of the zone of *B. praecursor*, s.l., and so are the forms characterized by the pronounced development of longitudinal markings and lack or feeble development of transverse to oblique vascular imprints.

Forms with longer ventral fissure, feebly ornamented to almost smooth conotheca, deep alveolus, short and somewhat bent bottom of ventral fissure are generally indicators of the upper half of the stratigraphical range of *B. praecursor*, s.l. Individuals with massive outline of the guard and more or less obtuse, mucronated apical end of the same, and those with vascular imprints dominating the longitudinal markings are also "high" forms. The importance of the character of the surface of the guard around the ventral fissure should be stressed, since most of the "high" forms carry at least a certain amount of longitudinal markings, a few weak transverse or oblique vascular imprints, or both, which does not seem to be the case with the "low" forms.

In attempting to distinguish between "high" and "low" forms, one should realize that all possible combinations of morphological characters may be encountered. The decisive factor is the predominance of "low" or "high" characters in a given specimen or specimens. The relative frequency of occurrence of these characters in a suite of specimens collected in any particular bed or layer presents an even better criterion, since out of a few specimens occurring together it is always possible to decide whether the bed in question is "high" or "low" in the zone of *B. praecursor*, s.l.

The suite of guards of *B. praecursor*, s.l., and its closest relatives reproduced in Pls. 56–58, is assembled so as to elucidate the concept of the species adhered to in this paper and to illustrate the most extreme morphological forms known to the writer. In the explanations to the plates each figured specimen is analyzed in its taxonomically important characters and assigned to one of the varieties and to "high," "low," or transitional forms of the species. No representatives of *B. praecursor* var. *praecursor* are included, as the figures of Stolley (1897) and of Müller and Wollemann (1906) illustrate this variety adequately.

The vertical distribution of certain morphological forms of *B. praecursor*, s.l., is not yet worked out in sufficient detail. The writer unfortunately lost most of his personal material of this species during World War II, before anything but the general outline of the vertical distribution of its morphological forms could be worked out. A pending study of numerous stratigraphically collected British individuals of the species will probably give him a chance to elaborate the above general remarks on the subject. Some amendments may also be necessary.

Paleogeographical variation

There does not seem to be much paleogeographical variation within *B. praecursor*, s.l. In England where the complete series of intermediate forms between *B. praecursor*, s.l., and *B. mucronata*, s.l., seems to be present, the morphology of *B.p.* var. *media* and *B.p.* var. *mucronatiformis* appears to be exactly like that of their Russian representatives. No representatives of *B. praecursor* var. *praecursor* are known to the writer from England, but this may be due

to the small number of guards studied rather than to its actual absence there.

In Germany, all hitherto described guards of *B. praecursor* belong to the extreme, smooth variety *B.p.* var. *praecursor* and a clear-cut separation of *B. praecursor* Stolley from all other *Belemnitella* forms appears to be possible despite the find of "a typical *B. mucronata*" together with it at Broitzem (see Stolley, 1906, pp. 92–93). If *B.p.* var. *media* and *B.p.* var. *mucronatiformis* are really absent in Germany, *B.p.* var. *praecursor* should probably be more properly classified as a geographical subspecies. It is of course possible that this typical *B. mucronata* belongs in reality to one of the other varieties of *B. praecursor* and that the extreme scarcity of this species in northwest Germany conceals its true range of variation and local relationships with *B. mucronata*.

All over the geographical range of *B. praecursor*, s.l., in European and Asiatic Russia no local forms were noticed.

Stratigraphical range of *B. praecursor*, s.l., and its bearing on the zones concept

The stratigraphical range of *B. praecursor*, s.l., may well differ in different parts of its geographical range (see Text-fig. 1 and earlier pages of this paper), as outside of the region of its evolutionary development, where the full record of *B. praecursor* was observed, only isolated evolutionary phases of this species were shown to be present. The observed relationships are exactly those of the complete biozone (=total zone of Fiege, 1951, p. 2589) of the species in the area of its evolutionary development as compared with the partial zones (=Teilzones) of the same in the periphery of its geographical range. This important theoretical concept of zonal correlation was developed by Pompeckj (1914, p. 35), Wedekind (1916, pp. 2, 53; 1918, p. 268) and H. Frebold (1924, pp. 315–320) and has been widely recognized and used since (e.g. Seitz & Gothan, 1928, pp. 12–13; Arkell, 1933, pp. 32–34; Fiege, 1951). In the case of *B. praecursor*, s.l., however, not only the partial zones of the species on the periphery of its geographical range, but also the extent of its complete biozone in the region where the evolutionary development of earlier *Belemnitella* forms has taken place, are known. This makes it possible to compare both ranges and to check the validity of the concept.

The upper time limit of the complete biozone of *B. praecursor* in European Russia is fairly well established. The rapid, geologically speaking almost abrupt, replacement of this species by *B. mucronata* (Schlotheim) mut. *senior* Nowak, s.s., takes place at about the top of the local zone of *Pteria tenuicostata*. Jeletzky (1948b, p. 592, Beilage 1) has shown that the boundary between the zone of *Pteria tenuicostata* and that of *B. mucronata* mut. *senior* is somewhat below but rather close to the boundary between the lower and upper Campanian. The coincidence is close enough to consider both boundaries as approximately contemporary for the purposes of the broad interregional correlation. The zone of *B. mucronata* mut. *senior* also was shown to agree more or less closely with the widespread ammonite zone of *Hoplitoplacenticeras vari* (Schluter) and *Hamites phaleratus* Grippenkerl (see Jeletzky, 1948b; Mikhailov, 1947, 1948).

The lower time limit of the complete biozone of *B. praecursor*, s.l., in European Russia is not quite as clear as the upper one and an attempt at its clarification is undertaken herewith.

Kabanov (1950, p. 129) has recently claimed that *B. praecursor* Stolley and *B. mirabilis* Arkhangelsky (i.e. *B. propinqua* Moberg non Arkhangelsky; see Jeletzky, 1949b) occur together in the zone of *I. pachtii* in the vicinity of the town of Ulianovsk (formerly Simbrisk). The writer suspects, however, that here *B.* ex gr. *B. mirabilis* was mistaken for the true *B. praecursor*, s.l. These two forms are, indeed, easy to mistake for one another unless the internal features, such as the depth of the alveolus, ornamentation of the conotheca, and the character of the ventral fissure, are considered. Kabanov's (1950, p. 129) paper, and specifically his treatment of the preserved ventral fissure in his *B. mirabilis* as a diagnostic distinction from *Actinocamax propinquus* Moberg, indicate clearly that he was not aware of these distinctions.

Arkhangelsky (1912, p. 196–197 and elsewhere) assumed that *B. praecursor* is characteristic of the whole succession of beds between the zone of *Inoceramus involutus*

Sowerby and the horizon carrying *B. mucronata* and *Actinocamax mammillatus* Nilsson (i.e. of his zones of *I. pachtii* and *P. tenuicostata*). The writer believes that also in this case *B.* ex gr. *B. mirabilis* and other predecessors of the true *B. praecursor*, s.l., were lumped together with this latter species. Jeletzky (1948b, p. 592–593, Beilage I) has, indeed, shown that *B. praecursor*, s.l., certainly does not occur in lower and middle parts of the zone of *I. pachtii* (=*cardissoides* beds), where its place is wholly occupied by its predecessors (see earlier pages, this paper). On the northeastern slope of the Dniepr-Donetz depression *B. praecursor*, s.l., appears only in the upper part of the *cardissoides* beds (=zone of *I. pachtii* of Arkhangelsky 1912), where it is accompanied by typical *Gonioteuthis granulata* (Blainville), such as occurs in the zone of *Offaster pillula* in England and in the upper *granulata* beds of northwest Germany (Jeletzky, 1948b, p. 592, Beilage I; 1951b, pp. 83–85). The occurrences of *G. granulata*, typical form, are, however, so rare and so uncertain as to their relative position within the upper part of the *cardissoides* beds, that the writer cannot be certain that this form occurs throughout their total thickness, as *B. praecursor*, s.l., most certainly does. On the northeastern border of the Donetz basin, where *G. granulata*, f. typ., is much more common and its stratigraphical range is better known, *B. praecursor*, s.l., appears somewhat earlier than that species. Here no *G. granulata*, f. typ., were found in the lower light-grey marls with *B. praecursor*, s.l. They first appear in the overlying bluish-green, clayey marls. Exactly the same relationships were met with by Krestovnikov (1924, p. 192) in the Great Don Bend where (author's translation from Russian)

> In the middle of the marls succession a phosphorite layer is present, which carries small black, and larger yellow phosphorites and the phosphoritized fragments of sponges. It separates the lower chalk-like marls with *Belemnitella praecursor*, *Pecten*, *Ostrea* etc., from the strongly clayey, greenish marls with *Pteria tenuicostata*, *Actinocamax verus*, *Actinocamax* of the type of *A. granulatus*, *Belemnitella praecursor*, etc.

There is little doubt that *Actinocamax* of the type of *A. granulatus* of Krestovnikov (1924) is the same as *Gonioteuthis granulata*, f. typ., on the northwest border of the Donetz basin, especially taking into consideration the complete agreement of both successions in all other respects. This suggests that also on the northeastern slope of the Dniepr-Donetz depression *B. praecursor*, s.l., appears somewhat earlier than *G. granulata*, f. typ.

It is well established by now that all beds with *Gonioteuthis granulata*, f. typ., be it upper *granulata* chalk of Germany or the lower part of the *Offaster pillula* zone in England, are equivalents of the lowermost zone of *Diplacmoceras bidorsatum* of the lower Campanian (see Grossouvre, 1901, p. 801; Muller and Schenck, 1943, p. 272) and younger than the upper zone of the Santonian stage with *Marsupites* and *Uintacrinus*. The above data, and also the association of *G. granulata*, f. typ., with *P. tenuicostata* in the upper marls of the Don Bend, show that the transmutation of earlier species of *Belemnitella* into *B. praecursor*, s.l., in the middle Russian boreal basin must have taken place somewhat earlier than the end of the Santonian epoch and apparently within the time of *Marsupites* and *Uintacrinus*. This event, which was not quite momentary at any rate, cannot be more precisely dated at the present time (see Text-fig. 1).

Jeletzky (1948b, p. 592, Beilage 1) has previously correlated the zone of *B. praecursor*, s.l., and *G. granulata*, f. typ., on the northeastern slope of the Dniepr-Donetz depression with the upper Santonian zone of *Marsupites* and *Uintacrinus*. Now, however, these beds in European Russia in general, and on the northeastern slope of the Dniepr-Donetz depression in particular, are considered as equivalent to the zone of *D. bidorsatum* and the Campanian-Santonian boundary is placed below them.

The known partial zone of *B. praecursor* var. *praecursor* in northwestern Germany is clearly within the above defined complete biozone of this species. Indeed, this form is associated at Broitzem in Braunschweig with all the index forms of the zone of *Diplacmoceras bidorsatum*, including the name fossil itself (Stolley, 1897, pp. 272–273, 299; Müller and Wollemann, 1906). The only guard of *Belemnitella praecursor* known from Westphalia, was apparently found in rocks of the same age, though Kahrs (1927,

p. 683) does not state in which part of the *granulata* chalk *B. praecursor* was found.

The partial zones of *B. praecursor*, s.l., in England are sufficiently well known. There, too, it is not known to descend into the zone of *Marsupites* and *Uintacrinus*, equivalent to the upper Santonian of France. The zone of *Offaster pillula*, in which *B. praecursor*, s.l., is common in Wiltshire around Salisbury, is characterized by *Gonioteuthis granulata*, f. typ., but not by its older forms (low forms) characteristic of upper Santonian, and is directly superimposed on the zone of *Marsupites* and *Uintacrinus* wherever this zone is developed in England. Thus, the partial zone of *B. praecursor*, s.l., in England may be correlated with confidence with the lowermost Campanian zone of *Diplacmoceras bidorsatum* of France and with the upper *granulata* chalk of Germany.

All the records of *B. praecursor*, s.l., from the higher parts of the *quadrata* zone (in the older and broader sense) of England, including that from the transition beds to the *mucronata*-zone in Hampshire (Rowe, 1900, pp. 345–346) and that from the *Inoceramus lingua* zone of Yorkshire (see Wright and Wright, 1942, p. 120), are still of lower Campanian age.

The isolated record of *B. praecursor*, s.l., from the borehole in Denmark is, so far as known to date, of about the same age as the German and English occurrences of this species.

Thus all partial zones of *B. praecursor*, s.l., known to date fall within its complete biozone. The principle of partial zones versus complete biozones appears, therefore, to be fully valid, at least in this particular instance, which makes *B. praecursor*, s.l., an exceptionally valuable "time marker" all over its paleogeographical range.

Paleogeographical distribution

The paleogeographical distribution of *B. praecursor* Stolley, s.l., appears to be extremely wide, wider in fact than that of most other *Belemnitella* species. In the U.S.S.R., this species commonly occurs all over middle, eastern and northern parts of European Russia, being common from the Urals in the east to eastern White Russia (Gomel district) in the west, and from the northern Donetz basin and Dniepr-Donetz depression in the south to the middle Volga and Ufa region in the north. *B. praecursor*, s.l., is equally common in the southeastern part of European Russia and in adjoining parts of Russian middle Asia (e.g. Mugojary, Caspian depression, Emba area, northern Kasakstan and even northern Kysil-Kum). Isolated occurrences of this species were reported from the eastern slope of Urals. On the Mangyshlak peninsula and further south *B. praecursor*, s.l., is not known to occur. It is also unknown southeast of northern Kysil-Kum, though it may occur in the Aral Sea area. Records of this species from the southern border of the Donetz basin (see Nalivaiko, 1935–36, p. 39) are erroneous. The writer was, indeed, able to study the specimens reported from here, which actually belong to upper Campanian slender forms of *B. mucronata* (Schlotheim). The writer knows of no authentic records of *B. praecursor*, s.l., from the Crimea or Caucasia, its reported occurrence in eastern Transcaucasia (Rengarten, 1940, p. 398) having been refuted as due to misidentification (Rengarten, 1953, p. 241). The guard in question has been found to belong to the late upper Campanian *Belemnitella langei* (Jeletzky, 1948).

The writer has seen one specimen of *B. praecursor*, s.l., from the marls in the vicinity of Schaulaj, Lithuania. It is sufficiently apparent that among *B. mucronata* recorded from the lower Senonian deposits of western and eastern Prussia by Spulski (1910, p. 60) and other authors, a fair amount belongs to *B. praecursor*, s.l. The writer has indeed seen several specimens of this species from these regions in the collections of the Geological and Paleontological Museum of the Humboldt University in Berlin. The writer believes (Jeletzky, 1948c, p. 345, 1949a, p. 266) that the *Belemnitella*-like form recorded by Ravn et al. (1913, pp. 100–101) and later by Lundgren (1934a, pp. 300–301) and Hagg (1947, p. 98, footnote) from the *quadrata* chalk of the borehole Groendals Eng in Denmark belongs to *B. praecursor*, s.l. This guard was indeed determined as *B. lanceolata* (Schlotheim) by Dr. G. C. Crick of the British Museum (Natural History), who appears to follow Blackmore (1896, pp. 529–530) (see also

Rowe, 1900, pp. 345–46, 1908, pp. 314–315 and Brydone, 1933, p. 286) in applying this name only to smooth, slender, and lanceolate to tapering *Belemnitella* forms from the English *quadrata* zone (in broad sense), which are synonymous with *B. praecursor*, s.l. The fact that "*B. lanceolata*" of Groendals Eng was encountered in the beds underlying the zone of *B. mucronata* (i.e. upper Campanian) makes it virtually certain the guard in question belongs to *B. praecursor*, s.l. and not to *Belemnella lanceolata* (Schlotheim).

B. mucronata (Schlotheim) mentioned by various Swedish authors from Kullemölla, Kvararännan (Mühlrinne) and Lyckas (see Moberg, 1885, 1894; Hagg, 1935, p. 65), and from the *Scaphites binodosus* beds of the borehole at Kullemölla (see Lundgren, 1934b, p. 8), are at least partly conspecific with *B. praecursor*, s.l. These Scanian localities are, indeed, of about the same age as the *Pteria tenuicostata* beds of European Russia (Jeletzky 1948b, pp. 593–595, Beilage 1) and the *quadrata* chalk of England, and geographically situated between these two main areas of occurrence of *B. praecursor*, s.l. Moreover, the writer has seen in collections of the University of Kiel (northwest Germany) two fragments of an adult *Belemnitella* form from the Lyckas marls collected by Dr. D. Wirtz, Hamburg, which are referable to *B. praecursor*, s.l., as known to him from the *P. tenuicostata* zone (lower Campanian) of European Russia, together with several indeterminable, juvenile *Belemnitella* guards, resembling those of *B. praecursor*, s.l. At the same time, it is not possible to identify the only specimen from Kullemölla figured by Hagg (1935, p. 65, pl. 10, fig. 9) with *B. praecursor*, even in the broad sense adhered to by the writer, since this guard is remarkably stout and possesses an obtuse, mucronated apical end. It probably belongs to one of the passage forms connecting *B. praecursor*, s.l., with *B. mucronata* (Schlotheim) mut. *senior* Nowak, s.s. The writer knows similar stout passage forms from lower Campanian rocks of both European Russia and England (see pl. 58, fig. 1a–c).

In Germany *B. praecursor* is known only from northwestern Germany and Westphalia. It appears to be totally absent all over Poland (except for the Baltic regions mentioned above), Podolia and Volynia. Also there is no record of this species from Pomerania, though some of the older records of *B. mucronata* from lower Senonian rocks of this province could conceivably belong to it rather than to true *B. mucronata*, s.l.

B. praecursor was never recorded from Belgium, Holland and France. Yet in England it suddenly reappears in relatively large numbers. Here it is common only in Wiltshire (Salisbury County, etc.). It also seems to occur in the northern area of England in Yorkshire. The reappearance of *B. praecursor*, s.l., in England strengthens the previously expressed opinion about its presence in Denmark, an area geographically intermediate between its Baltic (Prussia and Sweden) and English occurrences. *B. praecursor*, s.l., appears, thus, to be present more or less everywhere along the wide upper Cretaceous sea route of the Baltic sea, with its westernmost Eurasian records in England. It is evident that the starting point of this migration of *B. praecursor* was in the Russian basin of the boreal sea of Eurasia, since the evolutionary center of *Belemnitella* was definitely situated within this basin, and that the species has migrated in a westerly direction therefrom.

It is noteworthy that *B. praecursor* Stolley does not seem to have penetrated south of the middle Russian boreal basin. This appears to indicate much warmer climatic conditions to the south of the Donetz ridge, which was apparently raised above sea level at that time. Also, the penetration of *B. praecursor*, s.l., in a southeasterly direction and beyond the Urals seems to be rather limited. This is probably also due to marked changes in climatic conditions (warmer seas) rather than to impenetrable land barriers. There does not seem to be any reason to question the easy marine connection between Mangyshlak-Balchan and middle Asian seas on one hand and the seas of the Emba region and Caspian depression on the other. The faunal record, on the contrary, clearly indicates the pronounced climatic differences between these two groups of marine basins. The climatic zones of younger Upper Cretaceous epochs already have been discussed in detail elsewhere (Jeletzky, 1948b, pp. 593–595; 1951b, pp. 127–134).

It is remarkable that there are no records

of *B. praecursor*, s.l., from Arctic regions, though marine arms definitely extended northward along both slopes of the Urals connecting middle Russian and west Siberian marine basins with the upper Cretaceous seas of the Arctic. At that, marine beds with *Inoceramus* ex gr. *I. cardissoides* and *Pteria tenuicostata* Roemer, equivalent to the zone of *B. praecursor*, s.l., are already known at several localities within the European and Arctic regions of U.S.S.R. (Jeletzky, 1950b, pp. 22–24) and in Greenland (H. Frebold, 1934).

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EXPLANATION OF PLATE 57

All figures natural size

Belemnitella mucronata (Schlotheim), unnamed early variety. (p. 482)

FIGS. *1a, b*—Ventral and lateral views, University of Cambridge, Sedgwick Museum coll., no. B-1146. Upper Chalk, lower part of *mucronata* zone in restricted sense (lower part of upper Campanian, zone of *B. mucronata* mut. *senior* Nowak, s. s.). Whitecliff Bay, Isle of Wight, England.

This specimen, which is virtually complete in its alveolar part, belongs to a slender, elongated, and ventrally lanceolate variety of the species. In the form of its guard it is similar to the "high" form of *B. praecursor*, s.l., figured on Pl. 57, figs. 2a–c. Also the lack of intensification of the vascular imprints around the ventral fissure, except in its lower part, allies this guard with the last-mentioned forms of *B. praecursor*, s.l.

In its long ventral fissure, pronounced sculpture of the guard, and in the strong predominance of the transverse and oblique vascular imprints over the longitudinal markings, this specimen is indistinguishable from the typical representatives of *B. mucronata*, s.l. Apical end of the guard is broken off.

Such varieties of *B. mucronata*, s.l., are not known to occur below the upper beds of the *Pteria tenuicostata* zone (see Text-fig. 1).

Belemnitella praecursor Stolley var. *media* Jeletzky, n. var. (p. 497)

FIGS. *2a–c*—Ventral and lateral views and same specimen split longitudinally; author's coll. *Pteria tenuicostata* zone (lower Campanian); gray marls with *Gonioteuthis granulata* (Blainville), f. typ., *Actinocamax verus* Miller var. *fragilis* Arkhangelsky, *Pteria tenuicostata* Roemer, etc. Right shore of Desna River, 0.5 km. south of village of Pushkari, Chernigov Province, U.S.S.R.

The specimen shows the depth of the alveolus, the character of the ventral fissure, and the Schatsky index, which is 7.0–7.5 mm. in this specimen. Note the shortening of the bottom of the ventral fissure. The surface of the conotheca appears to be quite smooth to the naked eye, though a certain amount of fine ornamentation is actually present near the apex of the alveolus (compare Pl. 56, fig. 4).

This guard represents a "high" morphological form of the species, transitional to *B. mucronata*, s.l. The long ventral fissure, relatively pronounced vascular imprints on the alveolar part of the ventral side of the guard, and some intensification of the longitudinal markings and vascular imprints around the ventral fissure (fig. 2a), combined with a slender, nonmucronated outline of the guard, are characteristic of the "high" form of the species and of those transitional to *B. mucronata*, s.l.

3a, b—Ventral and lateral views, University of Cambridge, Sedgwick Museum coll., no B-65347. Upper Chalk, *quadrata* zone in a broad sense (Lower Campanian). Locality 1086, Southampton Waterworks new pit, Shawford, Hants, England. This specimen is referred to by Brydone (1912, p. 100), who collected it.

This specimen is transitional between that figured on Pl. 57, fig. 2, and that on Pl. 57, fig. 4. Morphologically it is a "middle" to "high" form of the species. Especially in the character of the bottom of the ventral fissure (see Pl. 56 fig. 1a) and in its relatively long fissure this guard approaches the "high" form of the species. In its feeble sculpture, predominance of longitudinal markings over vascular imprints, slender and acutely pointed outline of the guard, and in the virtually smooth surface around the ventral fissure, it is closer to the "low" forms of the species.

Such forms have been considered typical of "*Belemnitella lanceolata*" by Blackmore (1896) and Rowe (1902, 1908). Schatsky index on the original is 6.5 mm.

4a, b—Ventral and lateral views of holotype: author's coll.; same bed and locality as for fig. 2.

Though collected high in the zone of *B. praecursor*, s.l., this specimen is morphologically close to the "low" forms of the species, especially to those found near the bottom of the *Pteria tenuicostata* zone in European Russia. It is virtually indistinguishable from the specimen figured by Arkhangelsky (1912, pl. 9, fig. 1).

In its short ventral fissure, weak development of vascular imprints, fairly strong development of longitudinal markings, general outline of the guard, almost smooth surface around the ventral fissure, acute and nonmucronated end of the guard, and in the length and outline of the bottom of the vental fissure (see Pl. 56, fig. 2) this specimen is typical of the average ("mean") form of *B. praecursor*, s.l.

Belemnitella mucronata (Schlotheim) mut. *senior* Nowak, s. s. (p. 482)

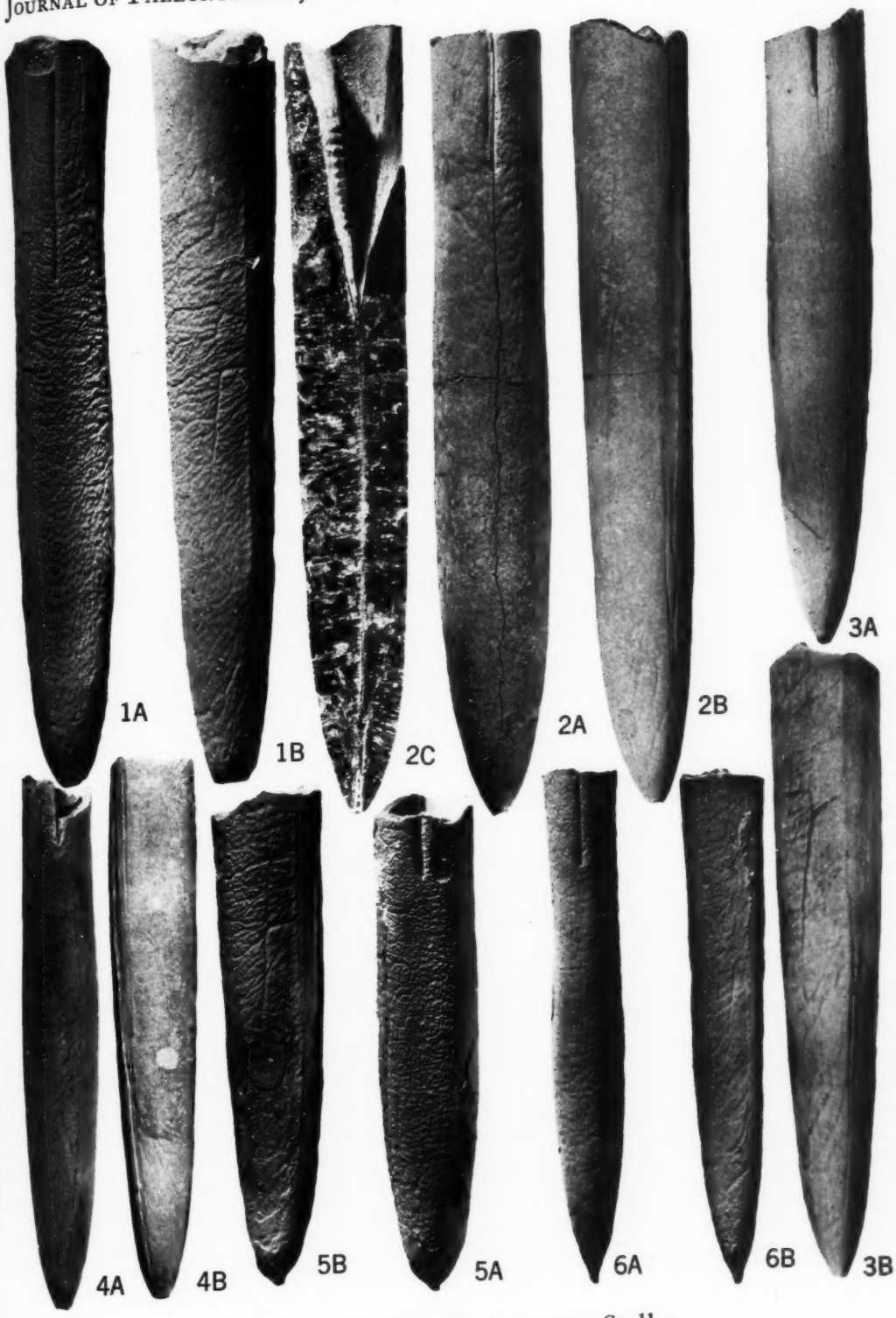
FIGS. *5a, b*—Ventral and lateral views, University of Cambridge, Sedgwick Museum coll. no. B-1145. Upper Chalk, lower part of the *mucronata* zone in restricted sense (lower port of upper Campanian, zone of *B. mucronata* mut. *senior*, s.s.). North of Kingstone, Dorchester, Dorset, England. Collected by A. J. Jukes-Browne.

A typical specimen of this form of *B. mucronata*, s.l., incomplete in its alveolar part. Note the obtuse, mucronated apical end of the guard and the strongly developed transverse and oblique vascular imprints with longitudinal markings suppressed by them. Vascular imprints are intensified around the ventral fissure, which is only poorly preserved; its greater length, as compared with that of *B. praecursor*, s.l., is nevertheless apparent.

Belemnitella mucronata (Schlotheim), s.l., var. (p. 482)

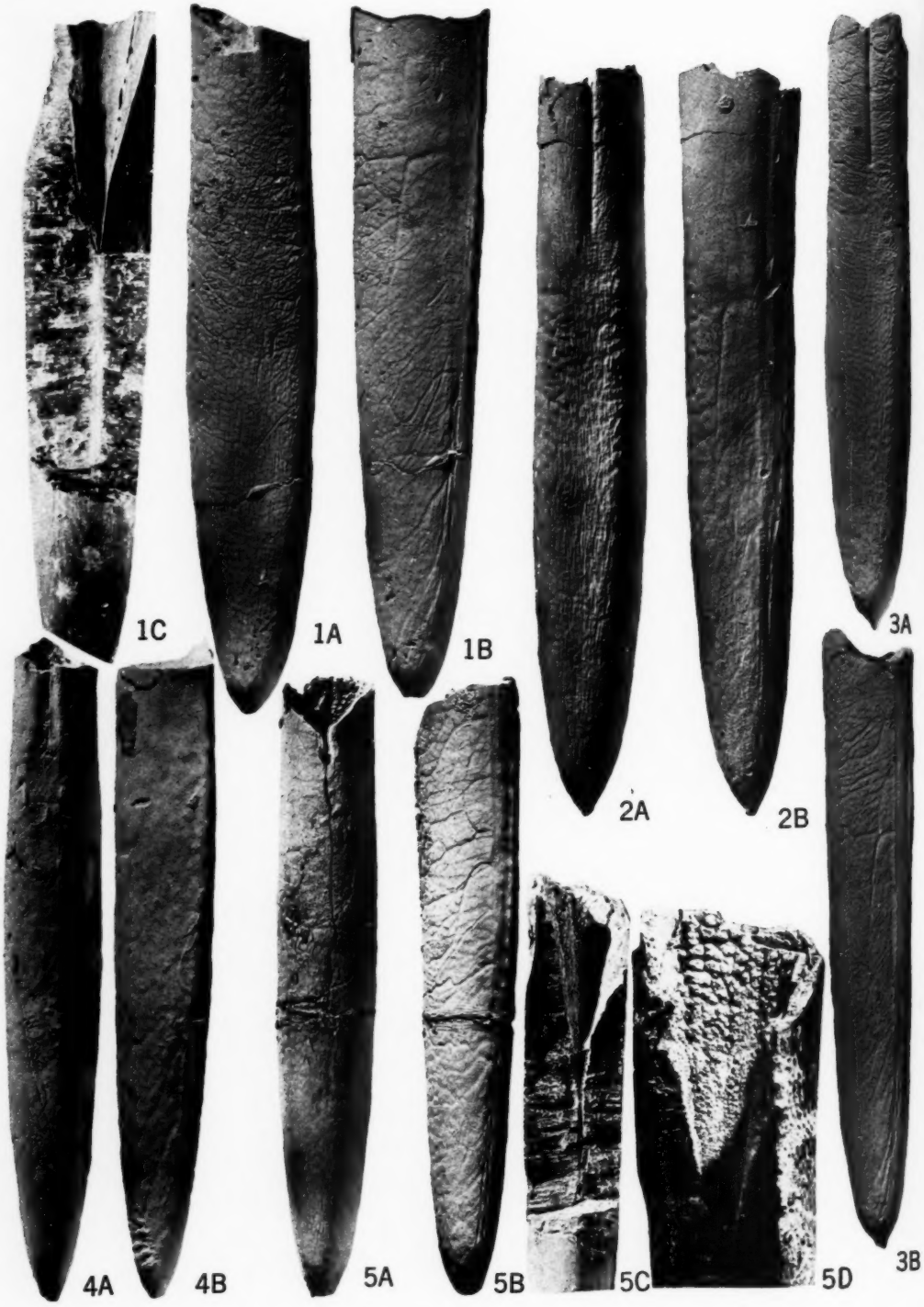
FIGS. *6a, b*—Ventral and lateral views, University of Cambridge, Sedgwick Museum coll. no. B-21449. Upper Chalk, *mucronata* zone in restricted sense (upper Campanian). Norwich, Norfolk, England. Probably collected from the upper part of the upper Campanian (*Bostrychoceras polyplocum* zone).

This slender, elongated, ventrally lanceolate specimen of *B. mucronata*, s.l., appears to be morphologically transitional between the slender, younger form of this species designated *B. mucronata* mut. *minor* by Jeletzky (1951b) and *B. lanceolatus* Sharpe (not Schlotheim or Blackmore). Both these forms are generally characteristic of the upper part of the *mucronata* zone above the beds abounding in *B. mucronata* mut. *senior* Nowak, s.s. (compare Text-fig. 1). The specimen illustrates the morphological differences between *B. praecursor*, s.l., and "recurrent" morphological forms of *B. mucronata*, s.s. Note the relatively greater length of the ventral fissure, predominance of the transverse to oblique vascular imprints over the longitudinal markings everywhere on the surface of the guard, and the intensification of the mesh of vascular imprints around the ventral fissure (fig. 6a). The apical end of the guard is rather acute, and so atypical of *B. mucronata*, s.l., yet it is distinctly mucronated.



Jeletzky, *Belemnitella praecursor* Stolley

FIGS.



Jeletzky, *Belemnitella praecursor* Stolley

EXPLANATION OF PLATE 58

All figures natural size unless otherwise indicated

FIGS. *1a–c*—*Belemnitella* ex gr. *B. praecursor* Stolley, s.l., Ventral and lateral views and interior view of the alveolus showing the outline of the bottom of the ventral fissure and the smooth surface of the conotheca; University of Cambridge, Sedgwick Museum coll., no. B-21457. Upper Chalk, junction of *quadrata* and *mucronata* zones (somewhat below the boundary between lower and upper Campanian). Coe's Pit, Bramford, Suffolk, England, Collected by J. V. Todd, Trinity, 1928.

The Schatsky index of this specimen is 7.5–8.0 mm. on the original. The part of the alveolus actually preserved amounts to four-tenths the preserved length of the guard; if the guard were more complete, the depth of the alveolus would be about forty-five hundredths of its length.

This somewhat incomplete specimen is transitional between *B. praecursor*, s.l., and *B. mucronata* mut. *senior* Nowak, s.s., and somewhat closer to the former species. The relative sturdiness of the guard and fairly strong development of transverse to oblique vascular imprints dominating the longitudinal markings and striae are more characteristic of *B. mucronata* mut. *senior*, However, the markings are distinctly weaker than in the latter, and the long, virtually straight outline of the bottom of the ventral fissure is more suggestive of *B. praecursor*, s.l., though similar outlines of the ventral fissure are common also in *B. mucronata* mut. *senior*. The relatively short ventral fissure, and the more or less acute and nonmucronated apical end of the guard are characteristic of *B. praecursor*, s.l. Such forms are common in the uppermost beds of the lower Campanian, but they are by no means absent in the older beds of the *Pteria tenuicostata* zone; they, however, become rare in the lower half of this zone. (p. 491)

2a, b—*Belemnitella praecursor* Stolley var. *mucronatiformis* Jeletzky, n. var., ventral and lateral views, University of Cambridge, Sedgwick Museum coll. no. B-21453. Upper Chalk, *quadrata* zone in a broad sense (lower Campanian). Whaddon, Wiltshire, England. Collected by A. J. Jukes-Browne.

This specimen is transitional betweeen the typical, distinctly sculptured forms of this variety (see Pl. 56, figs. 5a–d) and *B. mucronata* mut. *minor* Jeletzky, 1951, or the slender, hitherto unnamed from associated with *B. m.* mut. *senior* Nowak, s.s. (compare Pl. 57, figs. 1a–b). The predominance of the strong longitudinal markings and striae over the vascular imprints, weak development of the latter around the ventral fissure, and the slender outline of the guard, which tapers gradually apically, identify it as *B. praecursor*, s.l., while the relatively obtuse, fairly mucronated apical end of the guard, relatively strong sculpture, and a rather long ventral fissure are more characteristic of *B. praecursor* var. *mucronatiformis*.

Such forms are very rare or absent in the lower part of the *Pteria tenuicostata* zone but become rather common in its upper half. (p. 497)

3a, b—*Belemnitella mucronata* (Schlotheim), s.l., ventral and lateral views, University of Cambridge, Sedgwick Museum coll. no. B-21448. Upper Chalk, *mucronata* zone in restricted sense (upper Campanian). Hartford Bridge, Norfolk, England. Collected by H. Woods probably somewhere in the middle part of the *mucronata* zone below the beds with *Bostrychoceras polyplocum* Roemer.

This specimen is transitional between *B. mucronata* mut. *senior* Nowak, s.s., and *B. m.* mut. *minor* Jeletzky. Note its relatively shorter and sturdier guard with strongly obtuse and mucronated apical end, great increase of density of vascular imprints around the ventral fissure, and the equally strong predominance of the vascular imprints over the longitudinal markings and striae. The relatively great length of the ventral fissure is equally characteristic of *B. mucronata*, s.l. (p. 482)

4a, b—*Belemnitella praecursor* Stolley var. *media* Jeletzky, n. var., ventral and lateral views, University of Cambridge, Sedgwick Museum coll. no. B-65346. Same locality and collector as for specimen figured as Pl. 57, figs. 3*a*–b.

This specimen represents a slender, lanceolate form of the species, rather close to its average ("mean") representatives figured by Arkhangelsky (1912, see synonymy). The bottom of the ventral fissure (see Pl. 56, fig. 3) is, however, already somewhat shortened like that of the "high" form shown on Pl. 57, fig. 2c, and the fissure itself is somewhat longer than in the "mean" form of the species. The preservation of the guard is unsatisfactory and the character of the sculpture of its surface is, thus, difficult to appraise. It seems likely, however, that it is similar to the sculpture of the average ("mean") form of *B. praecursor* Stolley, s.l. As far as it is visible, the surface of the guard around the ventral fissure is quite smooth. (p. 497)

5a–d—*Belemnitella* ex gr. *B. mirabilis* Arkhangelsky, 1912 [*? = Belemnitella mucronata* (Schlotheim) mut. *anterior* Stolley, 1897]. *5a, b*, ventral and lateral views; *5c*, lateral view of the upper two-thirds of the guard with its alveolar part split off to show the inside of the alveolus; *5d*, oblique view of the inside of the alveolus, with ventral fissure in right foreground, ×2.

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This is a typical, fully grown, and nearly complete guard, It is generally similar to the average ("mean") form of *B. praecursor*, s.l., illustrated on Pl. 57, figs. 4a–b, in the form and sculpture of the guard. Note the strong development of the tranverse imprints, similar to those of *B. mucronata*, s.l. The view of the alveolus shows the characteristic ornamentation of the conotheca. Note also the somewhat lesser depth of the alveolus, amounting to 0.33–0.35 of the total length of the guard, and the irregularly bent, short bottom of the ventral fissure (fig. 5c). The Schatsky index on the original is 7.0–8.0 mm., which is the best distinction of this species from *B. propinqua* (Moberg), in which this character is not known to exceed 2.5–3.5 mm.

The peculiar ornamentation of the conotheca of the phragmocone is clearly visible on figs. 5c–d.

(p. 484)

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PALEOECOLOGIC OBSERVATIONS ON THE ORTHOCERATID COQUINA BEDS OF THE MAQUOKETA AT GRAF, IOWA

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ABSTRACT—The Graf, Iowa, Maquoketa exposure is restudied. The measured section stresses facies relationships of the lower, middle, and upper coquina beds. The paleoecology of the coquina beds is reconstructed based on faunal and lithologic evidence. Among other observations, laminated shales before and after the lower coquina bed are interpreted as due to an arythmical alternation of quiet and turbulent conditions.

The phenomenon of telescoping is examined in detail. Some of the findings are: telescoping is unlikely to be greater than 30–40 percent for most samples of the coquina beds; telescoped specimens can be classified into five groups which are defined and illustrated; retention of part of the original nacreous film on internal molds is thought to support the view that telescoping was accomplished before turbulent conditions and that it indirectly reflects shallow depths of water.

A sample of 326 fragments of *Dolorthoceras sociale* was collected systematically (i.e., with vertical and horizontal control of sampling interval). Histograms based on ratio of average segmental length and width indicate homogeneity of population both laterally and vertically. This, in turn, supports the interpretation that a single extended storm operative on a homogeneous population of *D. sociale* can account for the three coquina beds.

INTRODUCTION

THERE have been several studies of the Maquoketa exposure in the railroad cut near Graf, Iowa. Originally, Calvin and Bain (1899) and later, Thomas (1914) measured the section and reported on the faunal assemblage present. Miller and Youngquist (1949) studied the orthoceratid coquina beds and provided data on some new cephalopods as well as observations on telescoping.

The present study was first undertaken in 1951 to examine the phenomenon of telescoping in greater detail. In the early fall of 1953, the writer, with the help of Dr. Russell M. Jeffords, systematically collected material from the three coquina beds for the purpose of making a population study of *Dolorthoceras sociale*.

THEORETICAL CONSIDERATIONS

In a Recent Florida coquina, uniformity of size of the unaltered shell material was noted (Pettijohn, 1949, pl. 21A, opposite p. 302) and in an example of coquinoid rock, homogeneity of the population was observed (idem: pl. 21C). Doubtless, a whole spectrum of variation can be expected in different coquinas although homogeneity of the population is likely to be a persistent characteristic.

The coquina beds of the present study are composed dominantly of *Dolorthoceras sociale*. While endoceratids are also present, other cephalopods, such as *Beloitoceras* and *Probillingsites*, are sparsely represented. Numerous relatively small mollusks, etc. are found in these beds as well. Homogeneity of population should thus be construed to indicate the dominant species. The matter of uniformity or non-uniformity of fragment size will be discussed later in this paper.

STRATIGRAPHY AND PALEOECOLOGY

Stratigraphy.—In the 1951 study of the exposure, the section was measured at one station and blocks of the coquina beds sampled. As clocked off on an odometer, the studied portion of the exposure is 792 feet long. Thomas (1914) accommodated Bain's five orthoceratid beds in his remeasured section. However, in my measured section, only the three distinct coquina beds are designated. Thomas' bed 30: "cly sh, plastic, pebbleless, bluish-gray, breaks with a starchy fracture. Contains occasional flint chips and nodules. Grades into soil . . . 3 feet thick" was under a thick soil cover and was not observed. This bed apparently overlies the writer's highest bed, number 27.

Since the focus of this study is the coquina beds, the emphasis in the measured

section given below is placed on the facies relationships therein. The rest of the section is given in brief.

Paleoecology of the coquina beds.—Study of beds 18 and 19 of the above-described section indicates that somewhat different conditions prevailed during the deposition of the three coquina beds. To appreciate these conditions a survey is needed of the entire section (beds 1–17 and 20–27). On the bottom of the Graf portion of the Maquoketa sea, clay mud was deposited. Reducing conditions probably prevailed over patches of the bottom. This is suggested by the black color of the shales. Graptolites found in the lower beds support this interpretation.

Gravel-size pyrite nodules are found throughout the lower shales and pyrite crystals in orthoceratid septa and walls of the higher beds. Besides, numerous limonitic fossil fragments occur. The latter are certainly secondary. Ladd (1929) believed that all pyrite in the Maquoketa was of secondary origin. The pyrite nodules are also secondary, as field evidence suggests, though this does not exclude some generation of hydrogen sulfide in the postulated reducing environment of the lower black shales. Iron in solution at that time may

Maquoketa exposure, railroad cut at Graf, Iowa

Bed number		Thickness (in feet)
	Soil cover	
27	Brown sandy limestone (crystalline)	1.70
26	Brown finely-laminated shale	1.17
25	Brown arenaceous limestone, weathers gray	1.04
24	Brown platy shale	0.73
23	Buff-weathering arenaceous limestone, fossiliferous	0.75
22	Brown gray-weathering platy shale, fossiliferous	0.75
21	Buff-weathering arenaceous limestone	1.00
20	Brown-black laminated shale, weathers buff	1.33
19	Upper coquina (U) of *Dolorthoreras sociale* (one specimen, 8 inches long); fossiliferous arenaceous limestone; lower 5 inches laminated shale facies	1.25
18	Arenaceous dolomitic limestone containing the middle and lower coquina beds; subdivided into beds f–a, to preserve facies detail	2.70
	(f) Platy shale, black-brown, interbedded, gray weathering; upper portion finely laminated (2 in.)	
	(e) Finely-laminated black-brown shale (1½ in.)	
	(d) Argillaceous limestone containing some telescoped orthoceratids lower 1 inch black-banded, arenaceous shale facies (6 in.)	
	(c) Middle coquina (M) of *D. sociale;* arenaceous dolomitic limestone; black-banded arenaceous shale facies (4 in.)	
	(b) Dolomitic limestone, containing some telescoped orthoceratids; upper 6 inches markedly arenaceous (12 in.)	
	(a) Lower coquina (L) of D. *sociale;* coarse-textured argillaceous limestone (7 in.)	
17	Massive black-gray shale	0.29
16	Coarse-textured fossiliferous laminated shale	0.20
15	Massive gray-black shale	0.12
14	Arenaceous limestone, fossiliferous, coarse-textured	0.46
13	Platy black-brown shale, massive	0.77
12	Coarse-textured arenaceous limestone	0.58
11	Laminated calcareous siltstone, deep iron stain, fossiliferous	0.92
10	Fossiliferous calcareous gray shale	0.50
9	Fossiliferous calcareous laminated black-brown shale, weathers gray	0.39
8	Platy to thinly-laminated black shale, weathers gray; lower part same fossils as bed 7; 8 inches from top a limonite-hematite band	2.75
7	Fossiliferous limonitic brown-laminated mudstone weathers gray (resembles cement rock externally)	0.17
6	Thin, laminated to platy black shale, weathers gray	1.25
5	Same as bed 1. Deep limonite-hematite stain near top: thinly laminated (cf. to basal material of beds 1–3 which are massive). Top bed of this unit (2.50 in. thick) horizon marker and can be recognized by gritty surface of weathering.	2.91
4–1	Black platy shale at road level (bed 1) grading into black platy shale finely laminated at base containing pyrite nodules and deep limonite-hematite stain	4.20
	Total measured thickness	27.93

have been inadequate, or other chemical requirements insufficient, to result in primary formation of iron pyrites.

By the time bed 9 was deposited, some lime mud followed by silt and sand-size detrital quartz settled on the bottom.

Thomas (1914) reported that the beds at Graf were 15–20 feet above the top of the Galena. The writer, and earlier Ladd (1929) found limonitic *D. sociale* fragments in the basal Maquoketa. Thus, for the problem being discussed, this species must have been living in the Maquoketa sea from basal Maquoketa time on. Its absence or infrequent occurrence in the Graf beds older than 18-a, may, in part, be attributed to the reducing environment and perhaps the smaller amount of calcium carbonate in solution.

After deposition of a black-gray clay mud (bed 17), a considerable amount of lime precipitated from solution. Conditions for orthoceratid existence were thus restored and they must have been present in sizeable numbers in the sea. However, this statement should be qualified in light of the fact that the coquina beds consist of fragments of individuals. The largest fragment reported (2–3 feet long) for example, could, when broken, yield dozens of smaller fragments.

Also found on this bottom, and in the internal molds of the orthoceratids, are the early microscopic molts of trilobites (*Calymene*, for example), and numerous microscopic shells of *Spirorbis*. The latter have not been reported previously. In this connection, the occurrence of a zone of another tubicolous polychaete, *Cornulites*, at the top of the Brainerd, is of interest. Gastropods especially, were prominent in the coquina beds.

A block taken from the upper coquina bed, station 2 (see p. 517 for explanation), was mechanically broken down in a rock crusher. All cephalopod fragments and gastropods were carefully removed intact. Volumetric determinations were as follows:

To obtain an indication of the noncalcareous portion of the internal molds, a fragment of *D. sociale*, dry weight 12.93 grams, was dissolved in hydrochloric acid. An insoluble residue of 2.68 grams or 23 percent resulted. A few small silicified fragments of orthoceratids were found in the residue. This suggests that some original shell material was incorporated in the bottom muds and only later silicified. The above determinations indicate that for approximately 300 cc. of sediment from a coquina bed, about one-sixth of that volume was occupied by internal molds of *D. sociale*. Furthermore, better than 75 percent of this one-sixth was composed of calcareous sediment.

Once the internal molds formed on the bottom, they served as substrate for the encrusting bryozoan *Spatiopora iowensis*. *Endoceras* sp. fragments were also covered by this bryozoan. Remnants of the reticulate pattern are found on numbers of fragments.

In order to form a bed composed of thousands of fragmented internal molds of *D. sociale*, first the living individuals must die and the shells settle to the bottom. Then, the bottom mud with its benthos must fill the interior of the shells and indurate. After that, the original shell material must be dissolved leaving the free internal molds. Following that, the elongate conical internal molds must be fragmented. At this stage, there is still not a coquina bed. A mechanism is needed to heap these fragments onshore or nearer to shore. All sorts of variations on the above are possible. For example, the original shell may have fragmented before formation of an internal mold. As a matter of fact, only small portions of the living chamber are found on very few molds. Where preserved on specimens, the lower portion measured as follows: specimen 32, 9.99 mm., specimen 132, 24.55 mm. Thus, in most instances, it is doubtful if the entire living chamber remained intact long after the death of the animal. Bottom currents could fragment

	Volume (cc.)		*Per cent*	
Original block		295.00		100.00
(a) Cephalopods	44.00		14.90	
(b) Gastropods	4.00	48.00	1.30	16.20
Original block minus (a) plus (b)		247.00		83.80

the internal molds especially if they were over a foot long and perhaps incompletely hardened. However, to assemble in a helter-skelter heap tens of thousands of fragments in the range of 3.0 mm. to 83.0 mm., and occasionally some considerably larger, requires a mechanism of greater competence than the usual bottom currents in near-shore shallow water. Storm wave action has been postulated.

Thomas' faunal list for the Graf section shows that fragments of *Hyolithes* were "moderately common" in several of the beds, including the older shales, and recur in what is designated here as the lower coquina. It is of interest that no hyolithids were found in beds above the upper coquina, with the exception of Thomas' bed 21, a shale. In this bed, as well as in the older shales below the lower coquina, orthoceratids were reported to be "rare," and like the hyolithids, were not found in beds higher than Thomas' bed 21.

Hyolithid occurrence with benthos, such *Lingula*, in the older shales is anomalous since *Hyolithes* was a pelagic form. For similar examples in Upper Cambrian trilobite beds (Bonneterre dolomite, Warrior limestone), storm wave action was suggested as an explanation. This explanation agrees with the postulation of storm waves to account for the orthoceratid coquinas. It then follows, that even before, and on one occasion after deposition of the upper coquina, the quiet Maquoketa sea occasionally became tempestuous. The observations made above of hyolithidorthoceratid frequency and occurrence further suggest that had *D. sociale* been present in great numbers at times represented by pre- and post-coquina beds, additional coquinas would have been formed. The same waves that drove quantities of living hyolithids inshore and later hyolithid internal molds onshore, would have heaped up orthoceratid molds if they were present in quantity at such times. This, in turn, reflects the fluctuating density of the orthoceratid population in the Graf sector of the Maquoketa sea—greater density during the time leading up to the coquina beds, and lesser density before and after this population high.

If "storm waves" were the probable motor force, then, from one point of view, several storms seem necessary to explain the several coquina beds. Further, the Graf sector of the sea would have had to have been populated on successive occasions with *D. sociale*, the dominant species. The sequence given above, from death of animal to fragmented internal mold, would have to have been repeated in detail on successive occasions. The problems we are considering here did not confront earlier workers since facies relationships were not distinguished.

As will be shown in the later part of this paper, there is reason to believe that the *same* population of *D. sociale* (a topodeme). is represented in the three coquinas. The 12 inches of rock between the lower and middle coquinas, and the 9½ inches between the middle and upper coquinas may represent deposition in negligible periods of time. Thus, for example, bed 18-d and bed 18-c share a black-banded arenaceous shale facies and bed 18-f and 18-e may also, in part, be contemporaneous. Similarly, the arenaceous 6 inches of the dolomitic limestone of bed 18-b continues into 18-c. Bed 18-a and bed 18-b, as well as bed 18-c and bed 18-d, may also be nearly contemporaneous since telescoped orthoceratids were found in 18-b and 18-d. It is likely, therefore, that an extended single storm operative on the same population can explain the three coquina beds.

The heaping up of fragments onshore may have been preceded by the formation of elongate piles in shallow water. A series of huge storm waves could have then literally dumped this material onshore. Contemporary instances have been reported of hurricane wave action heaping up living bivalves by the countless numbers on a beach.

After deposition of the lower coquina, the occurrence of dolomitic limestone indicates an enrichment of magnesium salts in solution. This was accompanied by an increase in silt- and sand-size detrital quartz in the bottom sediments. Thus, both the dolomitic limestone and its shale facies are arenaceous. It is in the matrix of the limestone that the middle coquina occurs. No *D. sociale* fragments were found in the shale facies. It will be noted that by the time of deposition of bed 18-d, the argillaceous limestone of the lower coquina bed (18-a) recurs, and fragments of *D. sociale* are also present in 18-d. Thereafter, there was a marked de-

crease in calcium carbonate precipitation. Marked precipitation was not resumed until deposition of bed 19. Beds 20–28 did not contain any *D. sociale* fragments except in the single instance noted earlier.

If the several coquinas had first been elongate piles in shallow water, one could expect an argillaceous mud facies since this was the composition of the bottom in the Graf portion of the Maquoketa sea. Similarly, if storm waves heaped these piles on a sandy beach or close to shore on a sandy bottom, an increase of arenaceous sediment would be likely since this coarser detritus would compose the beach and/or nearshore sediments. In view of the lithologic relationships discernible in the rock record, it is reasonable to favor the above explanation of the sequence of events.

The presence of finely laminated shales (beds 18-e, 18-f, and 19, and in older beds such as bed 17) suggest interrupted sedimentation in quiet water. This interruption can be accounted for by a sporadic increase and decrease in electrolytes that would cause flocculation and settling on the bottom. It is of interest that preceding the lower coquina, and following the middle coquina extending into and beyond upper coquina time, such laminated shales occur. The quiet water indicated by the laminated beds forms a sharp contrast to the turbulent wave action suggested by the coquinas. Further evidence that the postulated wave action occurred in an irregular series of pulses is to be found in the arythmical alternation of quiet and turbulent conditions discussed above.

Telescoping.—A study of the phenomenon of telescoping should be preceded by some indication of the probable frequency of occurence. Table 1 provides these data.

From Table 1 it can be seen that double telescoping appears to have been more frequent than either triple or quadruple telescoping. Some 21.4 per cent of the total sample (n = 164) consisted of telescoped specimens. There is a possibility that telescoping may have been more frequent than the data indicate. In the writer's opinion, Table 1 represents a gross, rather than a precise, indicator of frequency. This may be so because chemical erosion by ground water may have dissolved the host fragment and left the invading fragment free. Evidence of such partial erosion of the hosts is found in many fragments. At least one curved specimen (no. 149 of this sample, see Fig. 1) at first appeared to be a single fragment. Microscopic study showed it to be four fragments telescoped together. Because of subsequent erosion, it simulated a single specimen.

TABLE 1.—NUMBER OF TELESCOPED FRAGMENTS OF *D. sociale* IN THE SAMPLE COLLECTED FROM SUCCESSIVE BEDS AT GRAF, IOWA (N = 164).

Bed number	Total specimens	Non-telescoped specimens	Telescoped specimens			
			Total	2[a]	3[b]	4[c]
19	19	16	3	2	1	—
18-d	38	27	11	11	—	—
18-c	37	29	8	3	3	2
18-b	13	9	4	2	2	—
18-a	57	48	9	9	—	—
	164	129	35	27	6	2

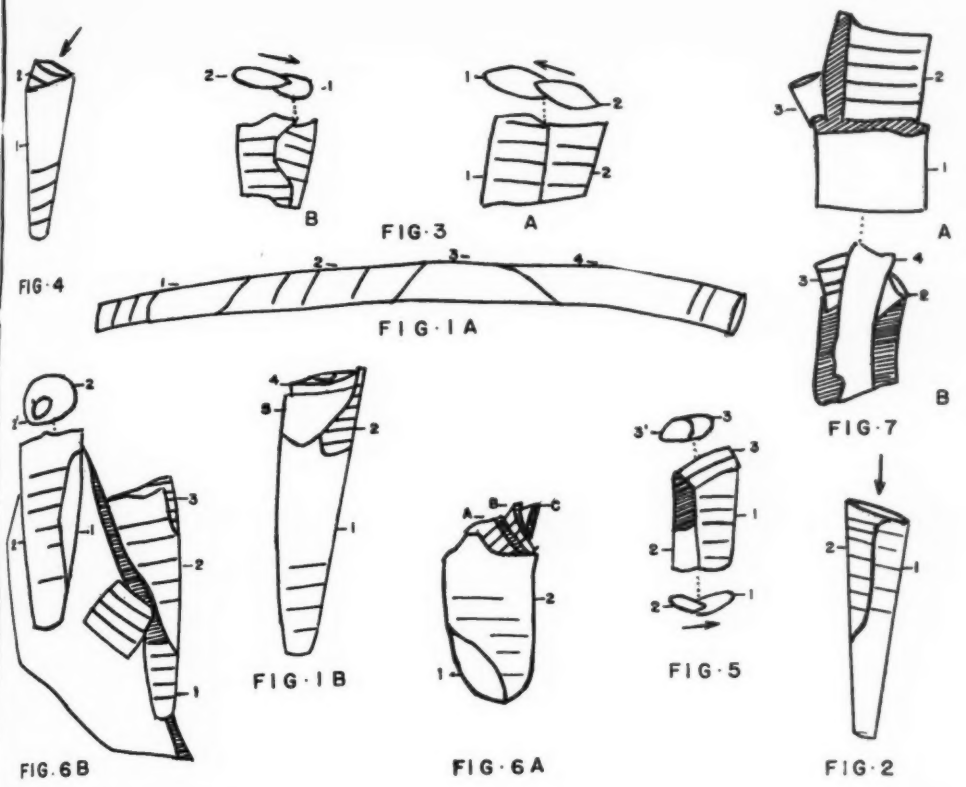
[a] Double telescoped.
[b] Triple telescoped.
[c] Quadruple telescoped.

Curved anomalies of this type would more readily be broken on the sea floor. Even so, telescoping is unlikely to be greater than 30–40 percent for most samples from these beds. These data should help to clarify our understanding of the phenomenon. It was not only a random event in this case, but was inoperative on most of the internal molds.

There still remain two aspects of the phenomenon requiring discussion: classification of the types of telescoped specimens, and consideration of the nacreous film preserved on internal molds.

Classification.—Figs. 1–7 were drawn directly from the telescoped specimens with the aid of a magnifying glass and a binocular microscope. These are schematic representations and are illustrative of the different kinds of telescoping observed. *D. sociale* is the main species involved even where, as occasionally occurs, *Endoceras* sp. or *Beloitoceras grafense* (cf. Miller and Youngquist 1949, pl. 41, fig. 4) are invader or host.

In most instances of telescoping all septal walls of the host fragment were found to have been dissolved and the host's interior completely hollowed out. This must have occurred after fragmentation of the internal



FIGS. *1–7*—Schematic illustrations of types of telescoped specimens in the coquina beds at Graf, Iowa.

1a, b—a, An example of quadruple telescoping of *D. sociale*. Specimen 149, Bed 18-c. Over-all length, 114 mm. *b*, Another example of quadruple telescoping. Specimen 132, Bed 18-c. Fragment 4 is *Endoceras* sp. Numbers 2–4 indicate successive invasions. Note that invaders may be hollowed out after entering hollowed-out host, and in turn, serve as hosts.

2—"Cone-in-cone" type of telescoping. Bed 18-d. Arrow indicates direction of invasion. Fragment 1 was host.

3a, b—Lateral invasion of flattened fragment into broken wall of host. Bed 18-c. Arrow indicates direction of invasion. In both *a* and *b* fragment 1 was host.

4—Oblique telescoping. Arrow indicates angle of invasion. Bed 18-d. Fragment 1 was host.

5—Compound telescoping. Bed 18-c. Flattened fragment 2 invaded the host, fragment 1. Elsewhere on sea bottom, fragment 3 was obliquely invaded by a slender fragment, *3′*. Then a fragment of 3 was cemented to the telescoped pair, fragments 1–2.

6a, b—a, An example of double telescoping and cementation to portion of living chamber of another fragment of a triple telescoped specimen (a, b, c). Bed 18-c. *b*, Slab showing a double telescoped specimen on the left (oblique type). *2′*, a slender fragment, invaded the host, fragment 2. Fragment 2 then invaded fragment 1. A triple telescoped fragment is shown on the right (oblique type). Note curvature developed when 3 invaded 2 (cf. Fig. 1a).

7a, b—Pseudo-telescoping. Bed 18-c. *a*, Fragments 1, 2, and 3 are cemented together. *b*, Reverse side of *7a*. Fragment 4 has been cemented to the other fragments. Superficially, this appears to be a case of multiple telescoping. Hatched lines indicate calcareous cement.

mold and may have been the control which accounts for the percent of telescoping observed. That is, potential hosts not hollowed out would have been less likely to receive invading fragments in their interiors. As discussed below, other types of telescoping would be possible even with all septal walls present.

Among the variety of forms of telescoping observed, what may be termed the "cone-

in-cone" type (Fig. 2) is infrequent. In this type, the narrow end of the invading fragment enters the wider portion of the host parallel to the host's walls. A high frequency of this type would require a remarkable degree of orientation of hollowed out fragments on the sea floor, and an even more incredible regulation of bottom currents to move precisely, unoriented invaders into hosts, always parallel to host's walls and most often, invading narrow portion first. It was the writer's doubts on this score that motivated this phase of the study.

A second type can be defined as lateral telescoping of a flattened invading fragment into broken walls of the host (Figs. 3a and 3b). A third type may be designated oblique telescoping (Fig. 4). Here, the invading fragment enters host at an angle. These two types are most common in the samples studied. The flattening of the invading fragment gave it a wafer shape and hence made it more readily subject to bottom currents than a doubly truncated cone. Angular invasion of the host fragment could take advantage of host fragments that were incompletely hollowed out and eliminate the need for unique orientation of hosts. These two types in particular, being most common, certify to the random nature of the telescoping process.

A fourth type, which one might expect to find occasionally, is pseudo-telescoping (Fig. 7). Fragments are cemented together and subsequent erosion simulates true telescoping.

Given the four types, a fifth category occurs, namely, compound telescoping (Fig. 5). Here, one or more of the other types of telescoping characterize certain fragments. In the illustrated figure, for example, lateral invasion of a host by a flattened fragment and also oblique invasion of a host occurred separately. This was followed by fragmentation of the last-mentioned telescoped fragment and cementation of a portion of it to the former telescoped specimens.

The variety of types of telescoping (cf. Fig. 6) gives evidence of considerable mechanical breakage of internal molds *after* telescoping and subsequent movement of such fragments onto other telescoped specimens. Instead of small rolling movements on the sea floor, this suggests something more akin to tossing around or impact between molds. It is likely that *telescoping was achieved prior to turbulence at sea* and that storm waves provided the energy for mechanical breakage.

Another line of evidence also seems pertinent to the above discussion. One of the impressive characteristics of many of the internal molds of *D. sociale*, even in those that are telescoped, is the presence of part of the nacreous layer of the original shell with faint pink, green, and cream-white coloration preserved. Many fragments are limonitic replacements, but all that are not, bear a powdery nacreous outer film. In measuring these fragments, the powder brushed off onto hands and lab coat and that alone sufficed to draw attention to its presence.

Any considerable movement from a place on the sea bottom, such as collisions between fragments, would probably have worn off the thin, nacreous film. However, since in telescoped pairs invading fragments often retain the film, it is plain that the movement accompanying telescoping one fragment into another must have been relatively free of friction. Otherwise, the wall of the invading fragment would have had the nacreous powder scraped off. The frictionless entry of invader into host seems curious since in most instances telescoped specimens show almost a "forced fit." It is likely that diagenetic effects may explain the "apparent" tightness. Nevertheless, preservation of the nacreous film in telescoped specimens further supports the reasoning given above, i.e., that storm waves fragmented already telescoped specimens. This indicates that telescoping was achieved on a hit-and-run basis by bottom currents in a relatively quiet portion of the Maquoketa sea. Only pseudo-telescoping may be attributed to great turbulence at sea. This interpretation differs from earlier ones which attributed telescoping to storm wave action (cf. Miller and Youngquist, 1949).

An additional inference follows from the presence of the original nacreous film. Foerste (1930) reviewed the literature on color patterns in fossil mollusks, including those of orthoceratids. By applying to fossil material observations on living mollusks (Forbes, 1844; Newton, 1907), he drew the

conclusion that distinct color markings on shells indicated access to light during the life of the animal. This, in turn, reflected the probable depth of water.

The zigzag color bands on orthoceratids that Foerste illustrated belonged to the upper layers of the shell. Quite differently, the colored nacreous film on the Graf internal molds was part of the inner portion of the shell wall. Nevertheless, it is reasonable to infer that the specimens Foerste illustrated originally possessed, besides the external color pattern, an inner nacreous layer. Conversely, the Graf orthoceratids probably had an external color pattern on the shell as well as an inner nacreous layer. If this assumption is correct, then Forbes' observations indicate that such distinct color designs denote shallow water. Newton went further. He showed that where only one out of 18 shells had color patterns, the depth was 100 fathoms (in the Mediterranean). Where more than one-half had color patterns, the depth was 2 fathoms or less.

If the frequency of external coloration of orthoceratid shells is indirectly reflected by the number of internal molds showing a nacreous film, then a high proportion of the population would have had external coloration. By Newton's criterion that would indicate very shallow depth.

STUDY OF GROWTH CHARACTERISTICS OF *D. sociale*

In the early fall of 1953, the writer in company with Dr. Jeffords, revisited the Graf exposure in order to take a systematic sample for a population study. Earlier, it had been thought that mechanical separation of intact fragments from blocks of the coquina beds might allow determination of presence or absence of fragment size uniformity. As the study of telescoping advanced, this appeared to be unfeasible. However, it served to point up a different but related question: Could any light be thrown on the growth characteristics of this species by systematic sampling of the three coquina beds and determining average length and width of individual segments?

In order to answer this question, the following procedure for sampling was employed. Eight telephone poles occur from the start to the end of the studied portion of the exposure. The relatively constant distance between each pole was 0.02 mile. Stations were set up at every other telephone pole. Thus, station 1 corresponded to the position of pole 1, station 2 to that of pole 3, etc. Four stations were set up corresponding to poles 1, 3, 5, and 7. The stations were approximately 0.04 mile apart. On a line roughly perpendicular to a given pole, the three coquina beds were sampled from lower to upper. This provided both horizontal and vertical control of sampling interval.

Although aware of the desirability of doing so, it was not feasible to collect equal samples from each horizon or at each station.

The frequency at which a given ratio of the average length and width of individual segments occurred would, it was thought, show little or no variation laterally but perhaps vertical variation would be noted. Fig. 8 summarizes these data. The ratio plotted refers to one of the growth characteristics of this species. A ratio of 0.40 denotes a small, slender fragment, while one of 0.16 (=0.20) a small, stout fragment.

The ratio of average segmental size and its frequency of occurrence at any horizon sampled is thought to reflect the number of stout or slender shells in the living population. This would hold even if the stout or slender portions of the conch corresponded to the ontogenetic development of individual orthoceratids. If at any time in the section studied, one or another of these types came to prevail, that would be reflected in a shift to right or left of the mean of the histogram. Fig. 8, while showing slight variations (i.e., at certain times there were a few more slender fragments than at others), in the main shows a persistent occurrence of the ratio 0.20, designating small, stout fragments. This persistence prevailed both laterally and vertically. This is interpreted to mean that a relatively homogeneous population of *D. sociale* is represented in all the coquina beds. Actually, if different populations were present (chronodemes), vertical variation might be expected.

The lateral and vertical persistence of fragments with a segment ratio of 0.20, all of which are small, stout fragments, may be

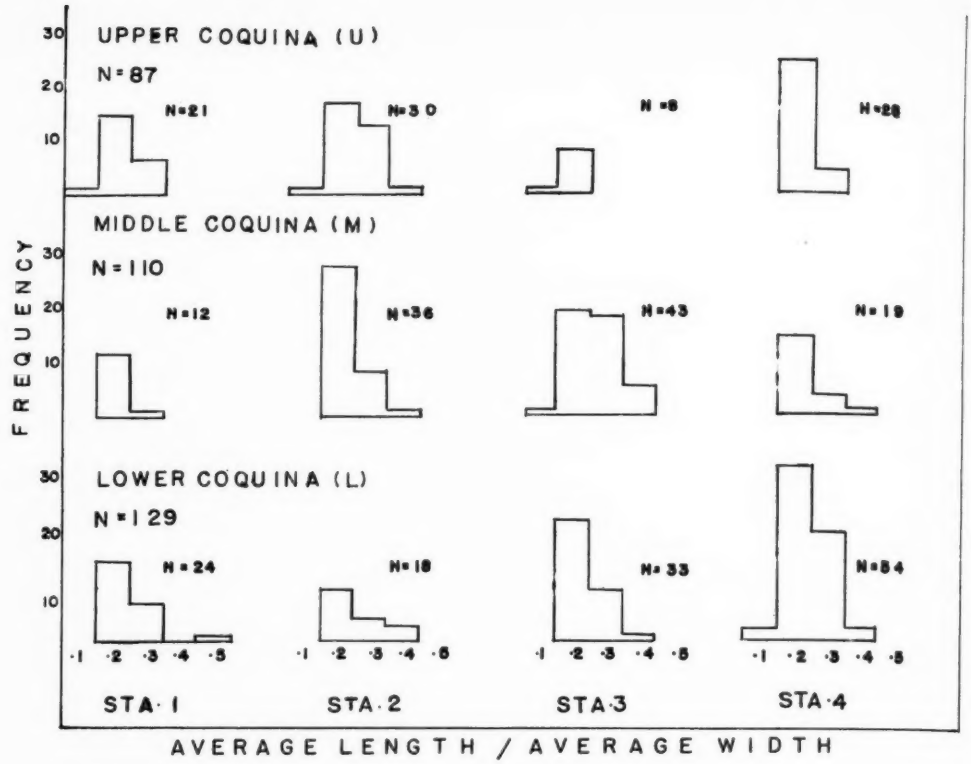


FIG. 8—Ratio of average segmental length and width for a sample of *Dolorthoceras sociale.*

related indirectly to fragment-size sorting. Although it is based on the available evidence, only this oblique suggestion is possible.

As stated earlier, Fig. 8 lends support to the argument that the same population contributed fragments for the three coquina beds. Relating this interpretation to the earlier discussion of one or several storms, it seems reasonable to postulate a single storm occurring in irregular pulses and operative on a single population of *D. sociale.*

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RODENTS FROM THE LOWER OLIGOCENE YODER FORMATION OF WYOMING

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ABSTRACT—A small collection of rodents from the Yoder formation of Wyoming includes a new genus of rodent of doubtful relationships: *Yoderimys* (type species, *Y. bumpi*, n. sp.). It is described as representing a new subfamily, Yoderimyinae, of the Eomyidae. The close relationships to undescribed material from the Vieja of Texas are pointed out and it is concluded that the Yoder is of earliest Oligocene age, slightly younger than the Vieja and older than the Chadron of Pipestone Springs, Montana.

INTRODUCTION

A SMALL collection of jaws and teeth of rodents was recently lent me for study by Dr. James D. Bump of the Museum of Geology, South Dakota School of Mines and Technology. This material (with one minor exception) came from a pocket about 4 by 5 feet in SDM Yoder Quarry No. 1, 4 feet above the floor of the Laramie Canal in the Springer Cut, NE ¼ Sec. 32, T. 23 N., R. 62 W., Goshen Co., Wyoming. The exception, an isolated incisor, came from the floor of the canal, 200 ft. west of Quarry No. 1.

During the past 25 years, a series of continental deposits have been described later than the top of the Uinta (upper Eocene) and earlier than the base of the Chadron (lower Oligocene). These include the Duchesne River formation of the Uinta Basin of Utah, its supposed equivalents of the Wind River Basin of Wyoming and of the Sespe of California, the Vieja of Texas and the Yoder of Wyoming. Unfortunately, all of these are either rather unfossiliferous, exposed in a limited area, or both, so that the described faunules are rather limited. Although a very considerable variety is known from the Vieja, most of the forms have not yet been described. As a result, there has been some disagreement as to the exact correlation of these horizons. Wood et al. (1941) represents the general consensus of mammalian paleontologists in placing the Yoder in the Oligocene and the Duchesne River in the Eocene. A revision of this work, now in process of compilation, does the same and considers the Vieja to be close to the age of the Yoder. While most students have considered that the Yoder is a distinct horizon antedating the Chadron, Clark (1937, pp. 327–328) considered that the Yoder should be considered the lower part of the Chadron.

All of the mammals hitherto described from the Yoder have been of medium or large size, including carnivores, perissodactyls and artiodactyls (Schlaikjer, 1935). Therefore the addition of this collection of rodents, even though limited both in number and variety, adds considerably to our knowledge of the total assemblage.

This study has been assisted by a grant from the Marsh Fund of the National Academy of Sciences.

Family EOMYIDAE
Subfamily YODERIMYINAE Wood, n. subf.

Diagnosis.—Eomyids in which P^3 has been retained; upper cheek teeth progressively characterized by an antero-posterior connection between the paracone and metacone along the buccal margin; mesoloph and mesolophid show variable but unusual attachments; anterior cingula of both upper and lower teeth very long; cusps plump and not reduced to narrow crests.

Discussion.—This subfamily is erected for two genera of rodents, an undescribed form from the Vieja of Texas, and *Yoderimys* Wood, n. gen., from the Yoder of Wyoming. The two are clearly closely related, probably in an ancestor-descendant relationship. It also is clear that these two are not closely related to any other hitherto described rodents. Their more distant relationships, however, are not so apparent.

At first sight they seem obviously to be-

long to the Eomyidae. P^3, however, is absent in all hitherto described eomyids. The absence of this tooth has generally been considered to be a familial character. Of course, it is obvious that forms that have lost P^3 were descended from ones where it was present. At the time such a transition was made, this presumably was only an individual variant, so that in ancestral forms the presence or absence of P^3 cannot be given the same weight as in later stages. The pattern of the lower teeth is suggestive of the eomyids, but, particularly in *Yoderimys*, there are striking differences in the structure of the mesolophid and protolophid, indicating that, if this form is an eomyid, it is very different from all previously described forms. Moreover, the known eomyids lack an anteroconid on P_4, whereas that cusp is very prominent in *Yoderimys*. There is no known eomyid whose upper cheek teeth at all resemble those of this genus. In all these respects, however, the Vieja form is intermediate between *Yoderimys* and the other eomyids.

Another possible allocation might be the Sciuravidae. The closest approach in that family to *Yoderimys* is in the middle Eocene (Bridgeran) genus *Mysops*. Here there is a small P^3, and the dental pattern is such that it *might* have given rise to that of *Yoderimys*. But there are very obvious differences, which make it impossible to feel sure of any actual relationship. This is natural in view of the time gap involved.

There are similarities to the Zapodidae, as represented by *Simimys* from the upper Eocene or *Schaubeumys* from the lower Miocene. But here P^3 and P_4 are lost and P^4 is reduced to a peg. No zapodids are known that are more primitive than *Simimys* in these respects. The tooth pattern is also quite different in detail.

Perhaps the tooth pattern is most suggestive of that of the Cricetidae, represented in the lower Oligocene by *Cricetodon* and *Eumys*. But no known member of this family had any premolars, and while they must have been descended from ancestors where that tooth was present, the gap here is rather large.

All other Eocene and Oligocene rodents that have been compared are very obviously different from the present form.

This leaves four possible allocations of *Yoderimys:* (1) as an aberrant eomyid, probably representing a new subfamily; (2) as a distant relative of the sciuravids, without more precise allocation; (3) as an even more aberrant zapodid, certainly representing a new subfamily; or (4) as the only known representative of a new family. The first of these three solutions is accepted as the most probable, although it must remain tentative until the discovery of adequate skull material. It is also possible that a combination of alternatives 1 and 2 indicates the true relationships, with *Yoderimys* intermediate between the sciuravids and the typical eomyids.

YODERIMYS Wood, n. gen.

Type species.—*Yoderimys bumpi* Wood, n. sp.

Diagnosis.—Cheek tooth formula P^3_1, M^3_3, the anterior upper premolar being peg-like; upper cheek teeth basically bipartite, with a union between protoloph and metaloph near center of teeth; strong buccal crest uniting protocone and metacone, and giving off a crest toward mesoloph; mesoloph weak; lower cheek teeth cuspate, with beginnings of development of crests; strong anteroconids on all teeth; ectolophid prominent and straight; mesolophid weak or replaced by pseudomesolophid; incisors with rounded anterolateral corners and enamel extending well onto lateral face; mental foramen high on side of mandible; masseteric fossa extending to beneath the rear of P_4 or front of M_1.

YODERIMYS BUMPI Wood, n. sp.
Text-fig. 1,A–G

Holotype.—SDSM 5330, lower jaw with P_4–M_3 left.

Referred specimens.—SDSM 5323, 5325, 5326, 53483 and perhaps 5328 and 5329.

Diagnosis.—As for the genus, considerable variation in connections between anteroconid and metalophid of P_4, in length of mesolophid of P_4, and in position of mesolophid of molars; mesoloph of upper teeth in process of splitting into buccal and lingual portions. Measurements as given in table.

Discussion.—The six specimens included in this species show a great deal of variability. But, for reasons outlined below, it

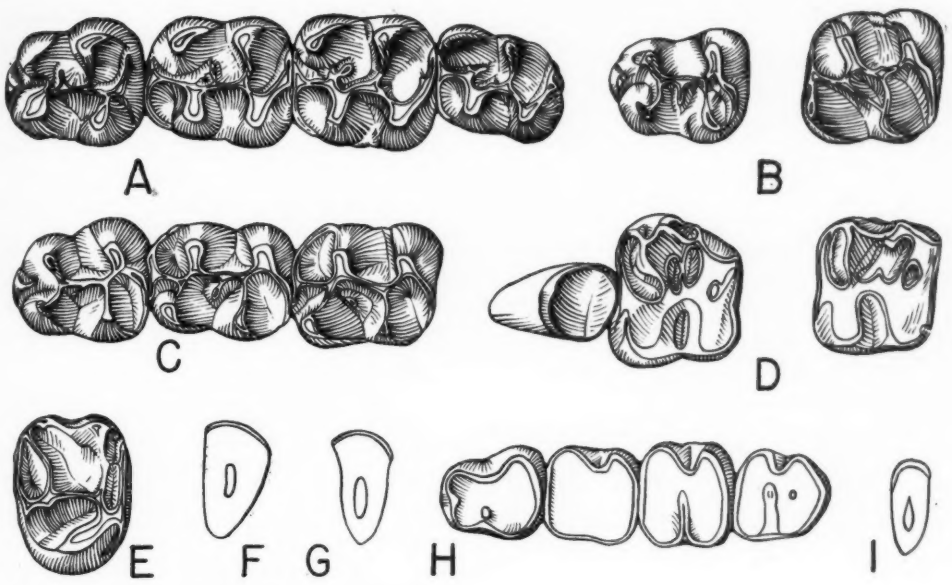

FIG. *1*—Teeth of rodents from the Yoder. All ×10.
A. *Yoderimys bumpi*, Wood, n. gen. n. sp. Holotype, SDSM 5330, P_4–M_3 left.
B. *Y. bumpi*. SDSM 5326, P_4 and M_2 right.
C. *Y. bumpi*. SDMS 5325, P_4–M_2 right.
D. *Y. bumpi*. SDSM 5323, P^{3-4} and M^2 left.
E. *Y. bumpi*, SDSM 53483, M^3 right. Anterior end to the right.
F. *Y. bumpi*. SDSM 5326, I_1 right.
G. *Y.* cf. *Y. bumpi*. SDSM 5328, I^1 right, seen from the rear.
H. cf. *Paradjidaumo* sp. indet. SDSM 5327, P_4–M_3 right.
I. cf. *Paradjidaumo* sp. indet. SDSM 5324, I_1 right, seen from the rear.

has seemed best to consider this to be one extremely variable species.

In P_4 there is a well developed anteroconid, from which a low crest extends backward to unite with the metalophid after considerable wear. However, in the holotype this crest runs to the metaconid, and in SDSM 5325 and 5326 it runs to the protoconid (Figs. 1A–C). The anteroconid is very much smaller in 5326 than in either of the other specimens. It is also much smaller in the Vieja form than in *Yoderimys*. In the holotype, the protoconid is a large, plump cusp, whereas in the other specimens it is transversely compressed. The mesolophid is a fair-sized crest in the holotype, slightly longer in 5326, but it is almost nonexistent in 5325, in which this specimen agrees with its relative from the Vieja. The entoconid is farther to the rear in 5326 than in either of the other specimens, and the hypoconid is distinct from the hypolophid at the stage of wear represented by this individual, which is not true of the other two. This difference is not entirely a difference in stage of wear. The posterolophid is long, reaching nearly to the lingual margin of the tooth in all specimens. In the holotype, there is a strong buccal continuation of this crest, absent or only suggested in the other specimens.

M_1 is present in the holotype and SDSM 5325 (Figs. 1A, 1C). In the latter, the anteroconid has a long lingual arm, reaching to the base of the metaconid, from which it is separated in the holotype. In both, there is a long, curved buccal extension of the anterior cingulum. In 5325, there is a metalophid running from the protoconid-anteroconid crest to a point half way up the slope of the metaconid. This crest is completely absent in the holotype, giving it a most unusual appearance. The referred specimen is in this respect intermediate between the rather aberrant holotype and the more

usual eomyid condition represented by the fossils from the Vieja. The mesolophid arises from the middle of the ectolophid in both specimens, in the normal rodent fashion. In the holotype, however, there is a slender crestlet extending from the tip of the mesolophid toward the protoconid, from which a similar crestlet has arisen. In view of the conditions in M_2, it looks as though these crests are about to shift the mesolophid from its normal attachment, forward to the protoconid. The posterolophid is a strong crest, without a buccal cingulum. On the holotype, there is a very faint basal cingulum along the buccal margin of the protoconid and hypoconid.

The second molar is present in three specimens. Here there is very extensive variation (Figs. 1A–C). The anterior cingulum is very long, reaching the base of the protoconid, and the anteroconid is large. In 5326 the metaconid has shifted forward almost to the anterior margin of the tooth, and is connected by a crest to the anteroconid. In the other specimens it has a more normal position, as in M_1. In 5325 the metalophid is essentially like that in the anterior tooth. In the holotype, there is a stubby metalophid arising from the protoconid, but it comes nowhere near reaching to the metaconid. In all specimens, the mesolophid has shifted its attachment from the ectolophid to the metalophid just in front of the protoconid. It looks as though this had occurred through piracy by the crestlets seen in M_1 of the holotype. No suggestion of this shifting is seen in the Vieja species. In 5326, not only has the mesolophid shifted its position, but it has considerably elongated, so that it reaches the entoconid, cutting off a central basin. This union of the mesolophid with the entoconid occurs in other eomyids, as, for example, in *Paradjidaumo minor* (Wood, 1937, fig. 49), although that form does not show the peculiar displacement of the buccal end of the mesolophid. In 5326, the mesolophid bears a small nubbin, which may or may not be what is left of the metalophid when the metaconid displaced forward. The hypoconid of 5326 is separate from the ectolophid, as in the premolar, and the hypoconulid is rather large. There is a buccal basal cingulum in the holotype, as in M_1. In 5326 the flat-bottomed basin between the protoconid and hypoconid is broader than in the other specimens.

M_3 is present only in the holotype, and is generally similar to M_2 of the same specimen. The metaconid is entirely independent, although there is a short nubbin of a metalophid pointing toward it. The mesolophid is firmly united to the metalophid, and slightly longer, proportionately, than in M_2. A small irregularity on the ectolophid looks like a mesoconid. The valley between the entoconid and posterolophid is widely open, and the latter bears an enlarged hypoconulid.

Of the upper teeth, SDSM 5323 includes LP^{3-4} and LM^2, of the same individual, and 53483 is an isolated RM^3 (figs. 1D–E). P^3 is very badly worn, and all traces of pattern have been lost. It is, however, a rather large tooth for P^3. As far as can be told, it was essentially conical. There is a deep transverse groove worn across the crown. In the three molars, the anteroloph is long, and extends across the entire front of the tooth, meeting the paracone on P^4 and M^2, and nearly meeting it on M^3, agreeing basically in this with its relative from the Vieja. The protocone and hypocone are separated nearly to the middle of the two anterior teeth, also as in the Vieja form. In P^4, the paracone is deeply notched, antero-buccally, and unites with the metacone, mesoloph, protocone and buccal cingulum. The mesoloph is fairly strong, and unites with a crest apparently from the paracone, although it may be a mesostyle. However, conditions in one specimen from the Vieja suggest that, in *Yoderimys*, the mesoloph has split in half, part being taken over by the buccal complex. The metacone is small and retreating, uniting with the mure, the posteroloph and the hypocone. This last is very large. M^2 is basically like P^4. The paracone is nearer the buccal margin of the tooth. The mesoloph is shorter than in the premolar, and is separated from the buccal cuspule, which here appears to be a mesostyle. Although the two are distinct, they are connected by plunging anticlines, so that they would join at a later stage of wear. The lingual valley is directed more forward than in P^4.

M^3 is much less worn than the other teeth, and is appreciably wider. There is no trace of a hypocone, the protocone being elongate along the lingual margin of the tooth. As in all the teeth referred to this genus, there is a strong antero-posterior crest running through the middle of the tooth. Anteriorly this unites with the protoloph, fairly close to the protocone. Posteriorly it reaches to the rear margin of the tooth, where it joins the lingual end of the posteroloph that extends laterally to the metacone and then forward to the paracone. From near the rear of the antero-posterior crest, a metaloph runs to the posteroexternal corner of the tooth, to a point that presumably represents the metacone, though there is a slight swelling of the buccal crest just anterior to this point. There is no indication of conules in this tooth, and presumably there were none in the other teeth. A low crest, not seen in the other teeth, unites the anterior cingulum with the middle of the protoloph. The protoloph is very far forward.

Lower incisors are present in SDSM 5325, 5326, 5329 and 5330 (Fig. 1F). They are all very much alike structurally, and agree almost exactly with the incisors of the yoderimyine from the Vieja. One specimen, 5329, is an isolated incisor. It is fifteen to forty per cent smaller than the other three specimens. While it is possible that this represents an additional species of *Yoderimys*, it is tentatively considered to be a juvenile.

An upper incisor, SDSM 5328, has an appearance rather like that of the lower incisors of *Yoderimys*, and may be tentatively referred here (Fig. 1G).

The differences among the lower teeth are such that the specimens might be referred to distinct species. Particularly SDSM 5330 and 5326 are very different, but 5325 combines features of both, together with ones of its own, so that it could not well be referred to either of the other species. The features of the jaws and incisors appear to be identical. The upper teeth likewise are quite different, 5323 and 53483 showing differences that could be considered to require that they be placed in separate species. But it seems improbable that a collection of three lower jaws from a single small quarry should belong to three species of the same genus, or that two specimens of upper teeth should represent two species. Furthermore, if the lower jaws were separated, it would be impossible to determine to which species the upper teeth should be referred.

For these reasons, it seems best tentatively to refer all these specimens to *Y. bumpi*, with the understanding that either more than one species is represented, or that it is a remarkably variable species. There is little doubt but that they are all congeneric.

The lower jaw is typically eomyid. The most notable features are the very high position of the mental foramen, almost up to the alveolar border, and the forward migration of the masseteric attachments, reaching to beneath the posterior end of P_4. A minute portion of the maxilla present on SDSM 5323 indicates that the posterior side of the zygomatic arch arose by P^4.

Measurements of Teeth of *Yoderimys bumpi* (in mm.)

Lower Teeth		Holotype SDSM 5330	SDSM 5325	SDSM 5326	SDSM 5329
P_4–M_3		7.51			
P_4	antero-posterior	2.05	1.96	1.87	
	width, metalophid	1.43	1.37	1.32	
	width, hypolophid	1.73	1.66	1.53	
M_1	antero-posterior	1.97	1.90		
	width, metalophid	1.60	1.46		
	width, hypolophid	1.75	1.57		
M_2	antero-posterior	1.94	1.92	1.82	
	width, metalophid	1.73	1.64	1.76	
	width, hypolophid	1.80	1.68	1.81	
M_3	antero-posterior	1.83			
	width, metalophid	1.55			
	width, hypolophid	1.43			
I_1	antero-posterior	1.51	1.45	1.55	1.12
	transverse	.97	.88	.91	.83

Upper Teeth		SDSM 5323	SDSM 53483	SDSM 5328
P^3	anterio-posterior	0.93		
	transverse	1.05		
P^4	antero-posterior	1.63		
	width protoloph	2.05		
	width metaloph	1.83		
M^2	antero-posterior	1.60		
	width protoloph	1.83		
	width metaloph	1.72		
M^3	antero-posterior		1.68	
	width protoloph		2.10	
	width metaloph		2.10	
I^1	antero-posterior			1.52
	transverse			0.80

Subfamily EOMYINAE, Wood, n. subf.
cf. PARADJIDAUMO sp. indet.
Text-fig. 1, H–I

A set of lower cheek teeth with a few fragments of the mandible (SDSM 5327) represent what appears to be an eomyid. The teeth are exceedingly badly worn, however, and little or nothing further can be told of them. In size, this specimen agrees closely with *Paradjidaumo minor* from the Chadronian of Pipestone Springs, Montana (Wood, 1937, p. 244), and may be tantatively referred to that genus.

An isolated lower incisor, SDSM 5324, is like that of *Paradjidaumo trilophus*, from the Brulé, and presumably belongs to the same form as do the cheek teeth.

Family PARAMYIDAE
cf. PROSCIURUS sp. indet.

An isolated incisor, SDSM 5322, is tentatively referred to this genus. Beyond indicating the probable presence of this Oligocene genus in the Yoder, it adds nothing. This specimen was found 200 ft. west of Quarry No. 1, at the level of the floor of the canal.

AGE OF THE YODER

The probable presence of *Paradjidaumo* and *Prosciurus* in the Yoder indicates Oligocene affinities, since neither of these genera is known from the Eocene, although close relatives of both are known from the Duchesne River. *Yoderimys bumpi* is the only Yoder rodent species known from material adequate to permit exact comparisons. There appears to be no known later form with which it can be closely compared. It is, however, very close to an undescribed form from the Vieja. There is no question but that these forms are closely related members of what seems to be a new group of eomyids. Structurally, at least, the Vieja form shows all the characteristics that would be expected in an ancestor of *Yoderimys*. The evidence of these specimens is clear that either the Vieja is older than the Yoder or that an ancestral form survived in Texas after its descendants had taken over in Wyoming.

Although it is impossible to be positive in the selection of one alternative, the former is here considered much more probable. How great a time gap should be allowed for the evolution of *Yoderimys* from its Vieja ancestor is problematic. But in view of the great amount of individual variation in both forms, it would not need to be great. In view of the absence of the Yoderimyinae from later deposits, there may be an appreciable gap between the Yoder and such early Chadronian deposits as Pipestone Springs. On the other hand, this may either represent merely an ecologic difference between the two areas, or the rapid extinction of the Yoderimyinae in post-Yoder time. The specimens of *?Paradjidaumo* and *?Prosciurus* do not actually give any very great support to a close tie-in with the Chadron. While it is difficult to be precise, perhaps the most probable interpretation of the rodent data would be to consider the Yoder as earliest Oligocene, somewhat nearer in time to the Vieja than to Pipestone Springs.

MANUSCRIPT RECEIVED OCTOBER 18, 1954

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JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 525–533, 3 TEXT-FIGS., MAY 1955

THE MINERAL COMPOSITION OF SOME MICROFOSSILS[1]

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ABSTRACT—The X-ray powder diffraction technique is well suited to determining the mineralogical composition of microfossils. By this means the original mineralogical constituents of the fossil or the nature of the minerals that have replaced the original shell material may be determined. Foraminifers and ostracods do not usually have to be crushed, as is ordinarily necessary for successful examination of most materials by means of the X-ray powder diffraction technique. Unreplaced perforate and imperforate foraminifers were found to be composed of either calcite or aragonite. From petrographic microscope studies, agglutinated foraminifers were found to incorporate the following substances in their walls: calcite, aragonite, quartz, feldspar, pyroxene, hornblende, magnetite, biotite, and volcanic glass. The shell material of foraminifers, ostracods, pelecypods, and gastropods was replaced by heulandite at several localities, in beds of Tertiary age. A midge pupa of Miocene age was found to have been replaced by analcite. The radular elements of *Nautilus pompilius* are composed of an indeterminate substance, not apatite.

INTRODUCTION

LITTLE is known about the mineralogy of fossils, particularly microfossils. This is partly so because most fossils are fine-grained mineral aggregates that are difficult to identify optically, and because chemical analysis requires a large sample and may be inconclusive. Moreover, optical or chemical identification methods require at least partial destruction of the specimen. The X-ray diffraction method of mineral identification, on the other hand, yields positive identification of the mineral constituents of microfossils without damage to the specimen.

The X-ray powder technique is now widely used, and the necessary equipment is readily available in most universities or research laboratories. However, since many paleontologists may not be familiar with X-ray diffraction procedures, the method is described here.

A preliminary examination employing routine optical methods using a petrographic microscope and immersion oils should be made. However, this method does not usually suffice when dealing with the fibrous aggregates comprising the tests of ostracods and foraminifers. Likewise, staining tests employing cobalt nitrate solution give less positive results than the X-ray diffraction procedure.

[1] Publication authorized by the Director, U. S. Geological Survey, and the Secretary, Smithsonian Institution.

THE X-RAY POWDER METHOD

Crystalline materials are made up of planes of regularly arranged atoms, which reflect X-rays in the way that a mirror reflects light. In the X-ray powder method the sample is composed of a fine-grained aggregate of randomly oriented crystal fragments and is placed before an X-ray beam in a suitably designed camera (see Text-fig. 1). Secondary X-ray beams are generated by reflection from the planes of atoms making up the crystals. The exact nature of the pattern of secondary beams developed depends upon the kind and arrangement of atoms making up the substance, hence each mineral species gives a different pattern. The patterns (Text-fig. 2) are like fingerprints in that unknown patterns may be identified by comparison with standards or with published data. A summary of X-ray powder data has been compiled in punch card form by the American Society of Testing Materials, Philadelphia, Pa. (the ASTM cards). However, since the mineralogy of fossils is relatively simple, most minerals composing fossils can be readily identified by comparison with a set of standard powder patterns.

A diagram of an X-ray powder camera is shown in Text-fig. 1. The pertinent features are: (1) collimator, producing a nar-

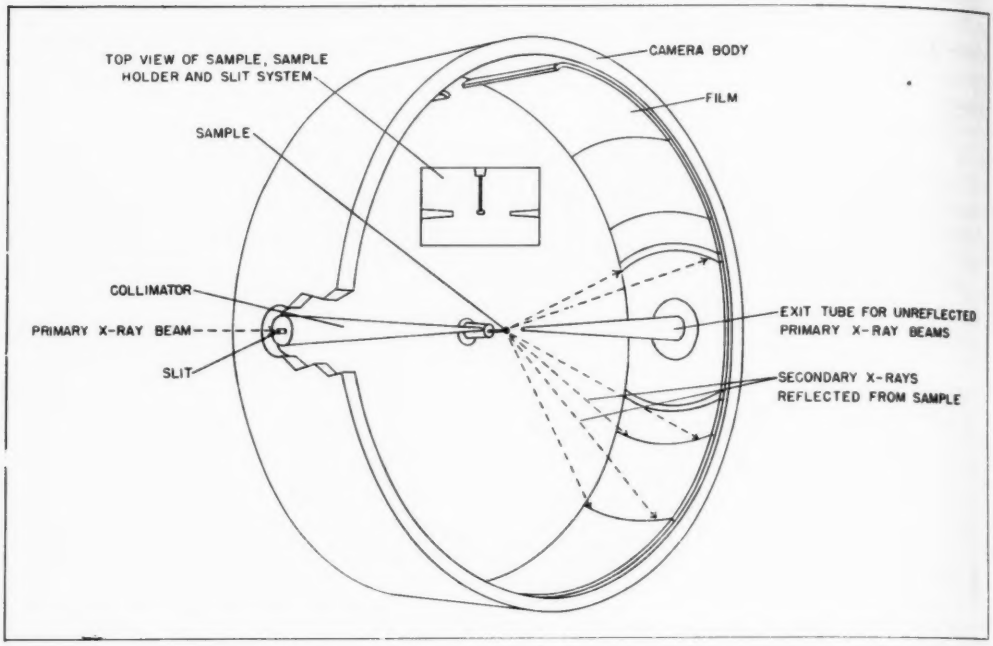

FIG. 1—Diagram of an X-ray powder diffraction camera.

row beam of X-rays; (2) sample, placed in the center of a cylindrical camera and rotated to accentuate the random orientation of the particles making up the sample; (3) exit tube, to trap the main unreflected X-ray beam so that it will not scatter and fog the film: (4) film, drawn tight against inner cylindrical surface of the camera; (5) a light-tight cover (not shown). The dotted lines show the secondary X-ray beams.

In practice the fossil specimen is mounted on the end of a fine glass fiber and placed in the camera so that just the specimen itself is in the X-ray beam. Because the material is normally fine-grained, the specimen does not usually have to be powdered. If it is larger than a few tenths of a millimeter in size, its height in the camera should be adjusted so that just the tip of the specimen is in the beam.

For most minerals copper X-radiation is suitable. For minerals having a high content of iron or manganese, iron radiation reduces fogging of the film due to fluorescence. For a camera 114 mm. in diameter, with copper radiation, an exposure of 3 to 5 hours is needed. For iron radiation the exposure must be somewhat longer.

Mixtures of minerals yield powder patterns consisting of the individual patterns of the minerals superimposed one upon the other; if the mixture is not too complex, it can be analyzed by the powder method. A concentration of a mineral less than 10 percent cannot ordinarily be determined by this method because only several of the mineral's strongest lines register on the film, and these are usually not enough for positive identification.

RESULTS

The reasons for investigating the mineralogical composition of fossil and Recent shells are twofold: (1) to determine the nature of the replacement product when a fossil has been mineralogically altered subsequent to its entombment, and (2) to determine the mineralogical nature of the original material when the organism has not been replaced or altered. The X-ray diffraction technique is ideally suited to treating these problems for the following reasons: (1) an extremely minute sample is sufficient, (2) crushing, sectioning, or dissolving of the specimen is usually not required, and (3)

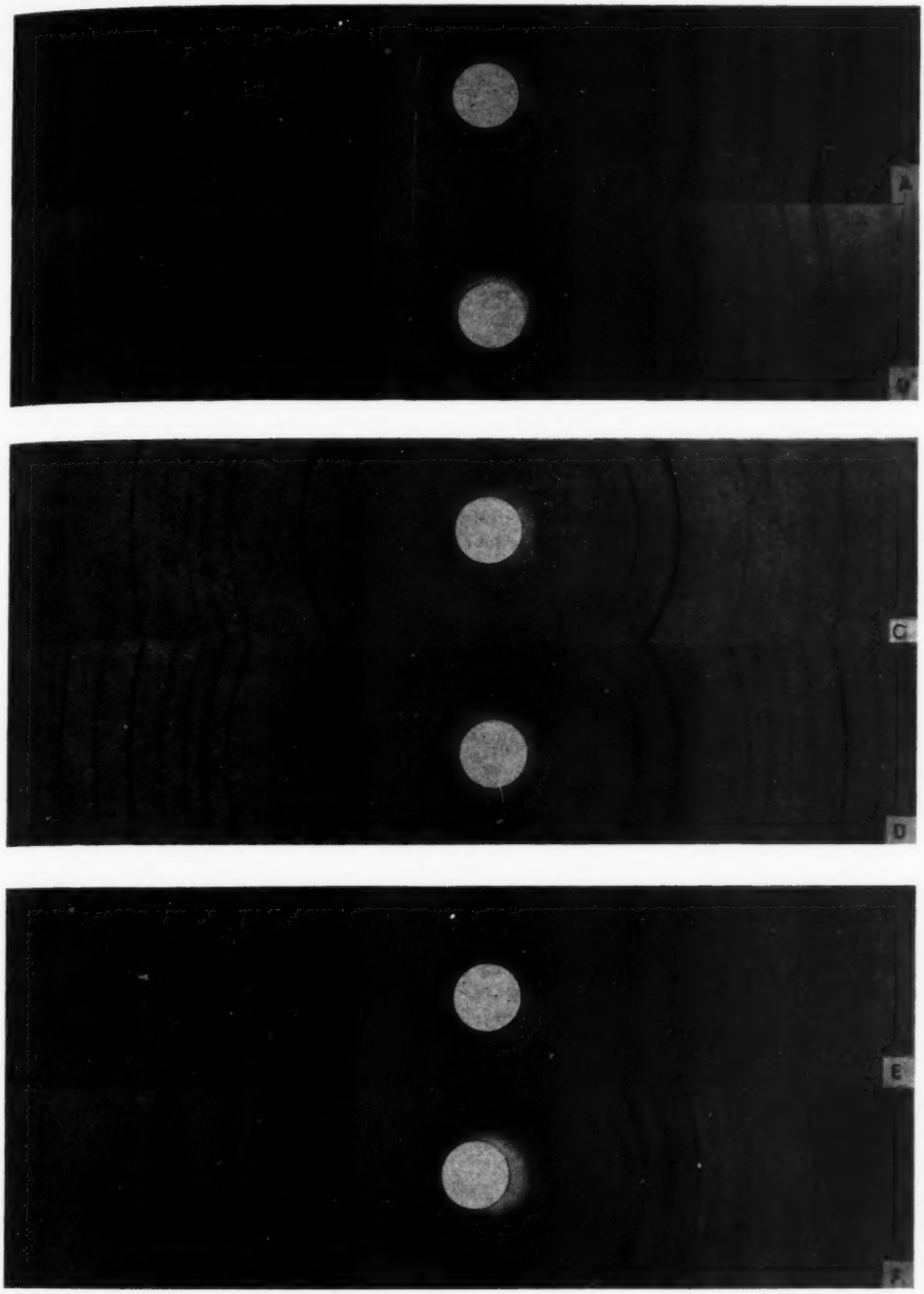

FIG. 2—Typical Diffraction patterns.
A. Calcite, Cape Province, South Africa. Specimen USNM 105765.
B. *Miliammina fusca* (Brady), NE Greenland. Sample no. 7.
C. Quartz—Herkimer, N. Y.
D. *Rzehakina epigona* (Rzehak) var. *lata* Cushman and Jarvis, Trinidad. Sample no. 11.
E. Heulandite, Berufiord, Iceland. Specimen no. USNM 85604.
F. *Globigerina* sp., Saipan. Sample no. 3.

the specimen is in no way changed morphologically by such an examination.

Several precautions must be observed. One possible source of confusion arises when a small specimen encloses a cavity that has been filled after death by a substance differing in mineralogical composition from the container. An example of this might be the articulated valves of a minute ostracod that, after death and subsequent decay of the organic material inside the two valves, has been filled with quartz particles of silt size. This specimen would give an X-ray diffraction picture indicating that the sample consisted of a mixture of quartz and calcite, whereas the shell consisted of calcite alone.

Table 1 summarizes the results of this investigation and gives an idea of the variety of minerals encountered in a random sampling of the material available to most paleontologists. Most of this material happened to be foraminiferal. Earlier, Mayer (1932) investigated by X-ray diffraction eight foraminiferal samples (*Orbitolites*, *Peneroplis*, *Miliolina*, *Globigerina*, *Nummulites*, *Operculina*, *Fusulina*). His samples were prepared by crushing the specimens; only calcite was found.

The X-ray powder method does not afford information as to the nature of the foraminiferal wall, i.e., it cannot be used to separate forms possessing differing wall structures unless they are composed of different minerals. The walls of agglutinated foraminifers are composed of a variety of substances including calcite, aragonite, quartz, feldspar, pyroxene, magnetite, hornblende, biotite, and volcanic glass. Some of the agglutinated forms contain such coarse grains that a satisfactory X-ray picture could not be obtained. Therefore, it was necessary to disaggregate the test by dissolving the calcareous cement with hydrochloric acid and examine the grains optically (Text-fig. 3). The specimen of the agglutinated genus *Bathysiphon*, composed of sponge spicules (Sample 28), proved to be quartz, although sponge spicules are usually reported to be opal. Previous workers (Heron-Allen and Earland, 1912, 1914) have reported agglutinated tests containing the following minerals: topaz, garnet, magnetite, and mica.

Species from 15 calcareous families were examined. Aragonite was not found among the forms selected from three imperforate families (Miliolidae, Alveolinellidae, Peneroplidae), but the small size of the sample does not rule out the possibility that some of the imperforate forms have aragonite tests. Species from 12 perforate families were examined; three (Cassidulinidae, Rotaliidae, Buliminidae) of these families were found to have both aragonitic* and calcitic species; whereas nine (Chilostomellidae, Nonionidae, Lagenidae, Globigerinidae, Nummulitidae, Amphisteginidae, Homotremidae, Globorotaliidae, Calcarinidae) were found to have only calcitic forms. It is not safe to assume, however, that these nine families will not be found to contain aragonitic forms when a more substantial sample is studied.

The occurrence of both aragonitic and calcitic species in the same families suggests that possibly a major revision of the classification is indicated. Possibly after further work the aragonitic forms will be found to comprise a major grouping of families comparable to the agglutinated and calcareous divisions of the present classification. However, some of the calcitic forms may originally have been aragonitic types that subsequently inverted to calcite. It is important therefore, that Recent material be relied on in investigating problems of taxonomic revision.

Two localities yielded perforate foraminifers that had been either replaced or filled by the mineral heulandite (Sample no. 1, 2). In the material from Tennessee, both replaced and unreplaced specimens of the same species were found occurring together. A few specimens were found in which only a part of the test had been replaced by heulandite. The replaced specimens from Tennessee had a distinctly hyaline appearance as opposed to the chalky or porcelaneous appearance of the unreplaced specimens. The

* Several determinations made in the course of this study have a bearing on the question of the stability of aragonite. Eocene and Upper Cretaceous foraminifers were found to be aragonite. Original pearly shell material of a nautiloid from the Deese formation of Pennsylvanian age (old asphalt mine, 3 miles south of Sulphur, Sec. 23, T. 1 N., R. 3 E., Oklahoma) was also found to be aragonite. Its unusual stability may be related to its entombment in asphalt.

TABLE 1

Sample no.	Mineral Identification	Fossil identification and stratigraphic horizon (p)—perforate wall (i)—imperforate wall (a)—agglutinated wall	Locality
1	Heulandite	*Cibicides* sp. (p); Paleocene	T-2-M (well); Tenn. Div. of Geology and U.S.G.S. test hole, located in picnic area of West Tenn. Agriculture Experiment Station near Jackson, Tenn.; 499–509 ft. down.
2	Heulandite	Ostracod; late Oligocene, Suwanee Is.	Washington County, Fla. Abandoned quarry in woods about 200 yards north of Duncan Church, in SE¼ sec. 36, T. 3 N., R. 14 W. (See Southeastern Geological Society, 1945) Collector, Eigle, 1945.
3	Heulandite	*Globigerina* sp. (p); Eocene, Hagman fm.	Saipan—interbedded flow-rock and tuff facies, Northeastern central Saipan. About 1540 ft., N. 50° W. from junction of East Coast Highway and Talofofo Road.
4	Calcite	*Robulus* sp. (p) (unreplaced); Paleocene	T-2-M (well); Tenn. Div. of Geology and U.S.G.S. test hole, located in picnic area of the West Tenn. Agriculture Experiment Station near Jackson, Tenn.; 483–499 ft. down.
5	Heulandite	*Robulus* sp. (p) (replaced); Paleocene	T-2-M (well); Tenn. Div. of Geology and U.S.G.S. test hole, located in picnic area of the West Tenn. Agriculture Experiment Station near Jackson, Tenn. 483–499 ft. down.
6	Calcite	Ostracod (dark-colored); Paleocene, Clayton fm.	Cut in Southern RR, 1½ miles out of Middleton, Hardeman County, Tenn. Collectors, L. W. Stephenson and Watson Monroe, 6/28/36.
7	Calcite	*Miliammina fusca* (Brady) (a); Recent	7 fathoms off Cape Stosch Gothoab, Hudson Land, Northeastern Greenland.
8	Calcite and unknown	*Dentalina? amchitkaensis* Todd (p); Early Tertiary	Outcrops in wave-cut bench 20–50 ft. wide, from 1–5 ft. above high tide. North coast of Amchitka Island, Aleutian Islands, Sample 43, 51°28′36″ N 179°08′15″ E.
9	Quartz	*Spiroplectammina brunswickensis* Todd and Kniker (a); Eocene Agua Fresca sh., middle part.	Brunswick Peninsula Magallanes Province, Chile. Well P-7, 1145–1147 meters deep.
10	Calcite	*Baculogypsina sphaerulata* (Parker and Jones) (p); Recent	A-1, Saipan, Mariana Islands.
11	Quartz	*Rzehakina epigona* (Rzehak) var. *lata* Cushman and Jarvis (a); Late Cretaceous (?)	Lizard Springs, Trinidad, British West Indies.
12	Heulandite	High-spired immature gastropod; Oligocene, Suwanee Is.	Washington County, Fla. Abandoned quarry in woods about 200 yards north of Duncan Church, in SE¼ sec. 36, T. 3 N., R. 14 W. (See Southeastern Geological Society 1945) Collector, Eigle, 1945.
13	Heulandite	Flat-spired gastropod; Oligocene, Suwanee Is.	Washington County, Fla. Abandoned quarry in woods about 200 yards north of Duncan Church, in SE¼ sec. 36, T. 3 N., R. 14 W. (See Southeastern Geological Society, 1945), Collector, Eigle, 1945.
14	Calcite	*Calcarina spengleri* (Gmelin) (p); Recent	Beach, Bikini Atoll, Marshall Islands. 11°36′45″ N., 165°32′59″ E. Bik 734.
15	Calcite	*Marginopora vertebralis* Blainville (i); Recent	A-1, Saipan, Mariana Islands.
16	Calcite	*Alveolinella* sp. (i); Recent	Depth of 50 feet off Eagle Island, Great Barrier Reefs, Australia. 14°39′ S., 145°21′ E. Collector, Capt. John B. Sloggett (Sample 6)

TABLE 1—*Continued*

Sample no.	Mineral Identification	Fossil identification and stratigraphic horizon (p)—perforate wall (i)—imperforate wall (a)—agglutinated wall	Locality
17	Calcite	*Calcarina* sp. (p); Recent	B-3, Saipan, Mariana Islands.
18	Calcite	*Globorotalia tumida* (Brady) (p); Late Tertiary	700–1000 fathoms, Guyot 200–300 miles east of Bikini Atoll.
19	Calcite	*Homotrema rubrum* (Lamarck) (p); Recent	Marshall Islands. 11°32′53″ N., 162°21′35″ E. Eni 11.
20	Heulandite	*Nuculana?* sp.; Oligocene, Suwanee Is.	Washington County, Fla. Abandoned quarry in woods about 200 yards north of Duncan Church, in SE¼ sec. 36, T. 3 N., R. 14 W. (See Southeastern Geological Society, 1945) Collector, Eigle, 1945.
21	Calcite	*Lenticulina* sp. (p); Jurassic, Lias	Septaena Bd., Wilflingen, Germany.
22	Calcite	*Amphistegina* sp. (p); Recent	Beach, Bikini Atoll, Marshall Islands. 11°36′45″ N., 165°32′59″ E. Bik 734.
23	Calcite	*Quinqueloculina* sp. (i); Recent	A-3, Saipan, Mariana Islands.
24	Calcite	*Heterostegina* sp. (p); Recent	B-6, Saipan, Mariana Islands.
25	Chitin?	*Nautilus pompilius;* Recent	Philippines.
26	Calcite	*Cycloclypeus* sp. (p); Recent	Dredging from 800 to 580 ft., off Bikini Atoll, Marshall Islands, 11°38′33″ N., 165°31′18″ E. Bik US 5949.
27	Augite, Hornblende, plagioclase, biotite, magnetite, glass	*Ammobaculites* sp. (a); Recent	494 fathoms, off Magabao Island, east coast of Mindanao, Philippines. 8°50′45″ N, 126°-26′52″ E. Alb. D5236.
28	Quartz	*Bathysiphon* sp. (a); Recent	39 fathoms, Atlantic Ocean, off Cape May. 38°01′15″ N., 73°44′00″ W. Alb. D2172.
29	Calcite	*Globigerinoides rubra* (d'Orbigny) (p); Recent	1917 fathoms, Atlantic Ocean, off eastern United States. 37°56′30″ N., 70°57′30″ Alb. D2097.
30	Calcite	*Dentalina? amchitkaensis* Todd (p); Early Tertiary	Outcrops in wave-cut bench 20–50 ft. wide, from 1–5 ft. above high tide. North coast of Amchitka Island, Aleutian Islands. Sample 43, 51°28′36″ N., 179°08′15″ E.
31	Calcite and unknown	*Astacolus* sp. (p); Jurassic, late Lias (=Taorcian)	Along south-facing hillslope about 3 km. NW of center of Andorra, Province of Teruel, southeastern part of Ebro Basin, Spain. Sf-5.
32	Calcite	*Nonion* sp. (p); Oligocene, Glendon Is. member of Byram fm.	West bank of Conecuh River at McGowan's Bridge, about 1 mile below the mouth of Sepulga River, Ala. USGS 6749.
33	Quartz and unknown	*Trochammina* sp. (a); Recent	494 fathoms, off Magabao Island, east coast of Mindanao, Philippines. 8°50′45″ N., 126°26′52″ E. Alb. D5236.
34	Aragonite and calcite	*Textularia* sp. (a); Recent	494 fathoms, off Magabao Island, east coast of Mindanao, Philippines. 8°50′45″ N., 126°26′52″ E. Alb. D5236.
35	Calcite	*Orbignyna ovata* Hagenow (a); Late Cretaceous, Campanian	Sassnitz, Island of Rugen, Germany.
36	Sponge spicules, pyroxene, hornblende, andesine	*Reophax* sp. (a); Recent	494 fathoms, off Magabao Islands, east coast of Mindanao, Philippines. 8°50′45″ N., 126°26′52″ E. Alb. D5236.

TABLE 1—*Continued*

Sample no.	Mineral Identification	Fossil identification and stratigraphic horizon (p)—perforate wall (i)—imperforate wall (a)—agglutinated wall	Locality
37	Pyroxene, hornblende, andesine	*Ammobaculites?* sp. (a); Recent	500 fathoms, off Atulayan Island, east coast of Luzon Philippines. 13°36′48″ N., 123°38′-24″E. Alb. D5469.
38	Pyroxene, hornblende, andesine	*Ammosphaeroidina grandis* Cushman (a); Recent	494 fathoms, off Magabao Island, east coast of Mindanao, Philippines. 8°50′45″ N., 126°26′52″ E. Alb. D5236.
39	Pyroxene, hornblende, andesine	*Ammobaculites?* sp. (a); Recent	494 fathoms, off Magabao Island, east coast of Mindanao, Philippines. 8°50′45″ N., 126°26′52″ E. Alb. D5236.
40	Aragonite	*Colomia californica* Bandy (p); Late Cretaceous	Kelleys Ranch near Carlsbad, California.
41	Aragonite	*Hoglundina elegans* (d'Orbigny) (p); Recent	100 fathoms, off Tampa, Fla.
42	Aragonite	*Ceratobulimina* sp. (p); Eocene, Claiborne group	1468 feet in L.O.R. Co. Tremont #2, Louisiana
43	Aragonite	*Ceratobulimina* sp. (p); Eocene, Claiborne group	Smithville, Texas.
44	Calcite and unidentified platy mineral	*Chilostomella* sp. (p); Eocene, Densinyama fm.	East side of Talofofo Road, 1600 feet S. 80° E. from juncture of Talofofo Road and Ridge Road, Northern Saipan.
45	Calcite	*Cassidulina* sp. (p); Recent	1–2 inches in submarine core from 410 fathoms, off Bikini Atoll, Marshall Islands. 11°41′00″ N., 165°14′01″ E.
46	Calcite	*Alabamina* sp. (p); Oligocene, Glendon (?) Is. member of Byram fm.	Rankin County, Miss. Robinson Quarry near Brandon, sec. 19, T. 5 N., R. 4 E.
47	Aragonite	*Ceratobulimina pacifica* Cushman and Harris (Holotype) (p); Recent	494 fathoms, off Magabao Island, east coast of Mindanao, Philippines. 8°50′45″ N., 126°26′52″ E. Alb. D5236.
48	Calcite	*Discorbis opima* Cushman (p); Recent	B-10, Saipan, Mariana Islands.
49	Calcite	*Reussella simplex* (Cushman) (p); Recent	E-6, Saipan, Mariana Islands.
50	Analcite	midge pupa, *Dasyhela?* sp.; Miocene	"adit bed," elev. 2650′, Mule Canyon, Yermo Quadrangle, center of NW¼, NE¼, SW¼ sec. 24, T. 10 N., R. 1 E., Calico Mountains, California.

specimen from Saipan (Sample no. 3) is a filling of heulandite in which even the minute perforations of the shell wall have been filled with heulandite and hence appear as fine spines.

The material from Florida yielded representatives from several phyla replaced by heulandite, including pelecypods, gastropods, and ostracods. The bed containing these replaced fossils could not have originally been overlain by more than 500 feet of post-Oligocene sediments (C. Wythe Cooke, personal communication, 1953), and no volcanic or hot spring activity has ever been suspected to have occurred in this region during the Tertiary. Therefore, it is evident that the heulandite was formed at normal ground-water temperature. Van Baren (1928) has reported heulandite from two soils in the East Indies, but has not proved that it is authigenic. Gilbert and McAndrews (1948) reported authigenic heulandite from a marine sandstone of late Miocene age in California. Bramlette and Posnjak (1944)

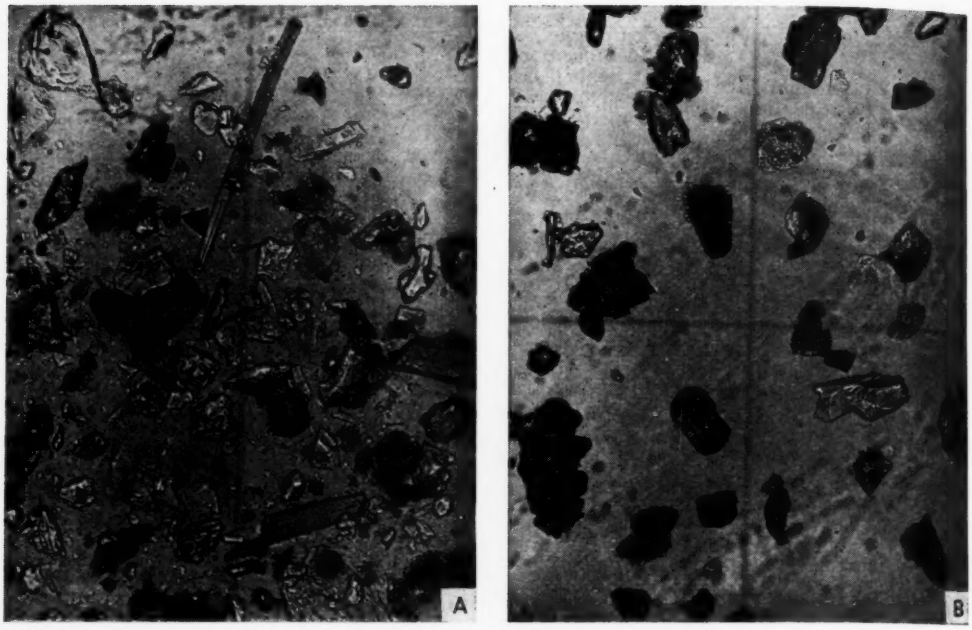

FIG. 3—Agglutinated foraminiferal tests disintegrated in hydrochloric acid and mounted in Canada balsam. ×50.

A. *Reophax* sp., Magabao Island, P. I. Grains are sponge spicules, pyroxene and hornblende (dark, high relief) and plagioclase (colorless, moderate relief).

B. *Ammobaculites* sp., Magabao Island, P. I. Grains are quartz (colorless, high relief), feldspar (colorless, low relief), volcanic glass (cloudy, moderate relief), and hornblende and augite (dark, high relief).

have reported clinoptilolite as an alteration product in vitric pyroclastic rocks.

W. F. Foshag communicates the following unpublished information regarding the occurrence of heulandite in limestone:

> Authigenic heulandite was identified in minute nests in a concretionary (algal?) limestone at Borate, Calico Hills, California. The limestone is a part of the Tertiary sedimentary series which also contains colemanite and gypsite, laid down partly under lacustrine, partly under playa conditions.

A midge pupa from beds of Middle Miocene age in the Calico Mountains, Yermo Quadrangle, California, collected and submitted by Allison R. Palmer, was found to have been replaced by analcite. To the best of our knowledge analcite has never been reported as having replaced fossils.

A dark-colored ostracod (Sample no. 6) was submitted for test by I. G. Sohn in the hope that the coloring material might be present in sufficient abundance to reveal its mineralogical nature to this technique. The amount of coloring material, however, was not sufficient for a determination.

Several radular elements from an alcoholic specimen of *Nautilus pompilius* were investigated because of their morphologic similarity to conodonts. It was felt that if the teeth of *Nautilus*, whose composition does not appear to have been previously investigated, are composed of apatite, as are condonts, one might have a bit of circumstantial evidence indicating the biologic affinities of conodonts. However, it was found that the teeth of *Nautilus* are not composed of apatite, but rather of a poorly crystallized substance (as evidenced by its weak X-ray pattern), possibly chitin. Radular elements of the squid *Loligo* had been previously investigated by Boucot with similar results.

Heron-Allen and Earland (1914, p. 1070) believe that foraminifers display both purpose and intelligence in their selection of

material. However, our own results (Text-fig. 2) indicate that, although certain genera may choose sponge spicules rather than sand grains, they do so through a preference for certain shapes. It is most unlikely that sand grains of the same shape and size but different mineralogic composition can be distinguished by the organism. We are led to this conclusion because of the random nature of the mineralogic composition in those agglutinated forms that incorporated pyroxene, hornblende, and feldspar into their tests. It was noticed that the percentage of these minerals in each test is variable, probably being a function of the random distribution of the mineral grains on the sea bottom. The characteristics of the mineral grains indicate that they may have belonged to a fall of andesitic volcanic ash.

ACKNOWLEDGMENTS

The writers wish to acknowledge the advice and assistance of Ruth Todd, of the U. S. Geological Survey, who suggested the problem, provided the bulk of the material, and identified the foraminifers. We also wish to thank Rucker Abbott, formerly of the Smithsonian Institution, for providing the radular elements of *Nautilus* and Orville L. Bandy, of the University of Southern California, Los Angeles, Calif., for calling our attention to certain specimens he had identified as aragonite. In addition we are grateful for the editorial assistance of Michael Fleischer and Charles Milton, of the U. S. Geological Survey.

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NOTES ON TERTIARY AND RECENT SOLEMYACIDAE

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ABSTRACT—A survey of the literature on the genus *Solemya* Lamarck reveals 23 Recent and 30 Tertiary species. The Recent species, referred to the subgenera *Solemya* s.s., *Petrasma* Dall and *Acharax* Dall are listed with data on their size and geographic and bathymetric distribution. Among the Tertiary species, three have been reported from the Paleocene of North America and Europe; eleven from the Eocene of Europe (France, Belgium, and Italy), Asia (India), and North America (Alabama, Georgia, South Carolina, and California); six Oligocene species have been described, from North America (Washington and Oregon), South America (Peru), and Europe (Germany and Belgium); seven species and two varieties are reported from the Miocene of Europe (Austria, Italy and Denmark), North America (Oregon and Costa Rica), Asia (Japan), and New Zealand; one Pliocene species has been described from Japan, and specimens referred to Recent species have been reported from the Pliocene of Italy and of California. One Miocene species has also been reported from the Pliocene of California. The only species described from the Pleistocene (Japan) has been referred to the synonymy of a Recent form. The genus *Adulomya* Kuroda is known from three species, all of Miocene age, in Japan.

Two new names are proposed: *Solemya* (*Acharax*) *prashadi* for *S.* (*A.*) *grandis* Prashad 1932, non Verrill and Bush 1898; and *Solemya stantoni* for the Jurassic *S. occidentalis* Stanton 1895, non *S.* (*Petrasma*) *occidentalis* Deshayes 1857.

While engaged in a study of the pelecypod fauna of the Keasey formation of the Oregon Tertiary, it became desirable to gather data on the known Tertiary fossil species of the genus *Solemya* and on the geographic and bathymetric distribution of the recent forms. The information proved to be so widely scattered in the literature that it semes worthwhile to record it here for the benefit of future students of the genus.

Genus SOLEMYA Lamarck, 1818

Solemya LAMARCK 1818, Anim. sans Vert., vol. 5, p. 488.
Solenimya BOWDICH 1822, Elem. Conch., pt. 2, p. 8.
Solenomya CHILDREN 1823, Quart. Jour. Sci., Lit., and Arts, vol. 14, p. 300.
Stephanopus SCACCHI 1833, Oss. Zool., vol. 1, p. 5.
Solenymia SWAINSON 1840, Treatise on Malacology, p. 366.
Solenymya SCHAUFUSS 1869, Moll. Syst. Cat. Paetel, p. 21.
Solemyarina IREDALE 1931, Rec. Australian Mus., vol. 18, p. 202.
Zesolemya IREDALE 1939, Brit. Mus. (Nat. Hist.) Great Barrier Reef Exped. 1928–29. Sci. Repts., vol. 5, no. 6, Moll., pt. 1, p. 232.
Solemyaria HABE 1951, Gen. Japanese Shells, pt. 1, p. 17 (err. pro *Solemyarina* Iredale).

Type species, by subsequent designation, Children, 1823: "*Solenomya*" *mediterranea* Lamarck = *Solemya mediterranea* Lamarck = *Tellina togata* Poli, 1791.

It being obvious that Lamarck formed the generic name *Solemya* as a combination of the Linnean generic names *Solen* and *Mya*, many authors have attempted to amend it with consequent confusion of the nomenclature. To this fact may be attributed the names *Solenimya* Bowdich, *Solenomya* Children, *Solenymia* Swainson and *Solenymya* Schaufuss as listed in the above synonymy. *Stephanopus* Scacchi, monotype species *S. polianus* Scacchi, is an absolute synonym of *Solemya* according to Bucquoy, Dautzenberg, and Dollfus (1898, p. 717). *Solemyarina* Iredale, type by original designation *S. velesiana* Iredale, is also a synonym according to Prashad (1932, p. 140) and Cotton and Godfrey (1938, p. 35). *Zesolemya* Iredale has as its type, by original designation, *Solemya parkinsonii* Gray, a species that Dall (see below) included in *Solemya* s.s. in his revision of the genus.

Dall (1908a, p. 1; 1908b, pp. 361–4) revised the then known Recent species. Basing his classification on the position of the ligament, he recognized three groups, which he distinguished as subgenera; these may be summarized as follows:

1. Ligament amphidetic, chiefly internal..... *Solemya* s.s.
2. Ligament opisthodetic, internal..... *Petrasma* Dall.
3. Ligament opisthodetic, wholly external..... *Acharax* Dall.

In this classification Dall accepted Bowdich's (1822, p. 8) usage of "*Solenimya*" *australis* as an example illustrative of the genus, as constituting a type designation for *Solemya* Lamarck, a procedure in which he has been followed by a number of more recent authors including Tegland (1933, p. 100), Thiele (1934, p. 791), Cotton and Godfrey (1938, p. 35), and Weaver (1943, p. 18). Habe (1950, p. 61) unaccountably states: "Type species: *Solemya australis* Lamarck (designated by Children 1823)."[1] Unfortunately Bowditch did not "select a type" in the strict meaning of that term as used in the International Rules of Zoological Nomenclature, and the first valid selection was that of Children, 1823, who designated *S. mediterranea*, the second species of Lamarck. The same species was cited by Gray (1847, p. 192) and "*Tellina*" *togata* Poli, the oldest valid name for the species was named as type by Herrmannsen (1848?, p. 481). The species was well illustrated by Fischer (1887, pl. 22, fig. 17) and by Bucquoy, Dautzenberg and Dollfus (1898, p. 717, pl. 92, figs. 8–10) who also give an extended synonymy. Its anatomy and systematic position have been discussed by Yonge (1939) in his study of the protobranchiate Mollusca.

The type of the subgenus *Petrasma* Dall (1908a, p. 2) is *Solemya borealis* Totten (1834, p. 366), that of *Acharax* Dall (1908a, p. 2) is *S. johnsoni* Dall (1891, pp. 712–3, 731). Both types are by original designation.

During the present study descriptions of twenty-three Recent species were found. Five of these are referrable, or have been referred by previous authors to the subgenus *Solemya* s.s., seven to *Petrasma* and ten to *Acharax*. One species, *S. africana* von Martens (1879, p. 742) has apparently been overlooked by subsequent workers, and the original description is inadequate to permit its certain assignment to a subgenus. Since, however, the original author indicates that the figure 2b of Reeve's illustrations of *S. mediterranea* represents his African species rather than the Mediterranean form, it is here temporarily listed under *Solemya* s.s.

It is interesting to note that Lamarck in 1818 knew of but two Recent species, and that Sowerby in his "Genera of Recent and Fossil Shells" (1822, pp. 85–86) mentions only the same two forms, while adding a notice of the first fossil species to be referred to the genus. Tryon (1872, p. 258) lists six Recent species in his "Catalogue of the Family Solemyidae" while Reeve in the Conchologia Iconica, pt. 320, *Solemya* (1875) gives but five species. Dall (1908a; 1908b) in his revision mentions fifteen Recent species.

The information that has been collected from the literature on the size and distribution of the Recent species is given in the following table. In the column on the size of specimens, the measurements are of the shell alone, without the periostracal prolongations; where marked by an asterisk (*) the data are those given for the type specimen of the species.

An examination of the table indicates that *Solemya* (*Solemya*) is primarily to be found in Australia-New Zealand waters; only the genotype species, present in the Mediterranean Sea and adjacent areas of the Atlantic Ocean, occurs outside of this area. Available bathymetric information is very scant, but indicates that it is primarily a shallow water form, though reported from depths up to 200 fathoms in Milford Sound. *Solemya* (*Petrasma*) includes small to medium sized species that have been found on both coasts of North America and in the West Pacific Ocean in Japanese waters. The species range through shallow to deep waters, being reported from 0–384 fathoms in the west Atlantic Ocean and from 0–860 fathoms in the eastern Pacific. In contrast, *Solemya* (*Acharax*) includes species that are predominantly of deep water distribution, although there is evidence that the controlling factor is water temperature. Thus *S.* (*A.*) *johnsoni* Dall has been reported

[1] I have not had access to Children's work to check this matter, but Kennard, Salisbury and Woodward in their paper on "The Types of Lamarck's Genera of Shells as Selected by J. G. Children in 1823" state that Children selected *S. Mediterranea*, adding that it was a new name for *Tellina togata* of Poli, 1795.

SPECIES OF THE GENUS *Solemya*

Solemya (*Solemya*)

Species	Size (mm.) Length	Height	Geographic distribution	Bathymetric distribution
1. *togata* (Poli) [1791, Testac. Utric. Sic., 2, p. 42, pl. 15, fig. 20] Synonyms: *solen* (von Salis) [1793, Reise ins. Koen. Neapel, p. 405, pl. 9, figs. 15A–B] *mediterranea* Lamarck [1818, Anim. sans Vert., 5, p. 489]	*38 93 (Bucq., Dautz. & Dollfus, 1898, p. 720)	14 27	Mediterranean & Adriatic Seas; Southeast coasts Spain and Portugal; Madeira and Senegal.	2–10 fathoms (Walther, 1894, p. 429)
2. *australis* Lamarck [1818, Anim. sans Vert., 5, p. 488]	57 (Cotton & Godf. 1938, p. 35)	26	South Australia, Tasmania (Cotton & Godfrey, 1938, p. 35) South Australia, New Zealand. (Dall, 1908b, p. 364)	Shallow water: "The animals have been observed leaping or swimming about in the water." (Cotton & Godfrey, 1938, p. 35.)
3. *parkinsonii* Gray *in* Smith [1874, Voy. Erebus & Terror. p. 6, vol. 3, fig. 1]	51	18	(see bathymetric distribution)	"Throughout New Zealand in fat mud about 6 inches below the surface, often washed up after gales; Kermadec Islands; Milford Sound in 100–200 fathoms." (Suter, 1913, p. 830).
4. *terraeregina* Iredale [1929, Mem. Queensland Mus., p. 262, pl. 30, fig. 13]	*11	4	North Queensland, Australia, from Capricorn Group to Torres Straits (Iredale, 1939, p. 232).	"I saw a living animal collected . . . by sandwashing on the reef." (Iredale, 1939, p. 233) 10–12 fathoms, Michelmas Cay; 17–20 fathoms, Goode Island; Torres Strait, Annam River, Starke River, Green Island, Masthead Island." (Iredale, 1929, p. 262)
5. *velesiana* Iredale [1931, Rec. Austral. Mus., 18, p. 201]	"always small" (Iredale, 1931, p. 201)		Sydney Harbour, Australia (Iredale, 1931, p. 201)	
(incertae sedis) 6. *africana* von Martens [1879, Monatsb. K. Akad. Wiss. Berlin, p. 742]	*61	21	Querimba Isl., coast of Mozambique.	

Solemya (*Petrasma*)

7. *borealis* Totten [1834, Amer. Jour. Sci. (2), 26, p. 366, figs. 1h, i]	*67	22	Halifax, Nova Scotia—Pensacola, Florida. (Dall, 1908b, p. 364). Nova Scotia to Connecticut (Johnson, 1934, p. 15)	Living animals 7–349 fathoms; empty shells 56–300 fathoms (Verrill, 1884, p. 278.
8. *velum* Say [1822, Acad. Nat. Sci. Phila., Jour., 2(2) p. 317]	20 *24	9	Halifax, Nova Scotia—North Carolina (Dall, 1908b, p. 364). Nova Scotia to Florida (Abbott, 1954, p. 333).	0–384 fathoms (Dall, 1889, p. 46); living animals 0–10 fathoms; empty shells 9–115 fathoms (Verrill, 1884, p. 279).
9. *occidentalis* Deshayes [1857, Jour. de Conch., 6, p. 137; 7, pl. 7, fig. 6]	7		Gulf of Mexico to Guadalupe Is. (Dall, 1889, p. 46). Spezzia, Tripoli, Morocco, Florida Keys, Old Providence Island, West Indies and Yucatan Passage (Dall, 1908b, p. 364).	0–5 fathoms (Dall, 1889, p. 46). 2–200 fathoms (Dall, 1908b, p. 364).
10. *panamensis* Dall [1908, Harvard Coll. Mus. Comp. Zool., Bull. 43, p. 366]	*38	15	Santa Barbara, California to Panama. Hertlein & Strong, 1940, p. 378 8° to 37° North Latitude. = Panama Bay to Santa Cruz, Calif. (Keen, 1937, p. 25).	30–60 fathoms (Dall, 1908b, p. 364). 29½–68 fathoms (Dall, 1908b, p. 366). 860 fathoms (Durham, 1942, p. 121) "in mud flats at extreme tide, rare, La Paz" (Pilsbry and Lowe, 1932, p. 141). 10 fathoms, Punta Penasco, Sonora, Mexico (Lowe, 1935, p. 27).
11. *valvulus* Carpenter [1864, Ann. & Mag. Nat. Hist., (3), 13, p. 311]	*22	6.5	San Pedro, California, to Punta Penasco, Mexico (Hertlein & Strong, 1940, p. 378) 23° to 37° North Latitude [=Gulf of California to Santa Cruz, California] (Keen, 1937, p. 25)	10 fathoms, Punta Penasco, Sonora, Mexico.

Species	Size (mm.) Length	Height	Geographic distribution	Bathymetric distribution
12. *pusilla* Gould [1861, Boston Soc. Nat. Hist., Proc. 8, p. 27]	8.9	3.2	Kyushu, Honshu and Southern Hokkaido, Japan, (Habe, 1950, p. 63)	"5 fathoms, mud" (Gould, 1861, p. 27)
13. *pervernicosa* Kuroda [1948, Jap. Jour. Malac., 15 (1–4), p. 32, text figs. 4–5]	*53	21	Off Cape Erimo, Hokkaido, Japan. (Habe, 1950, p. 63)	
			Solemya (*Acharax*)	
14. *johnsoni* Dall [1891, U.S. Nat. Mus., Proc. 14, p. 189; 17, pp. 712–3, 731, pl. 25, fig. 1]	*112 73 (Woodring, 1938, p. 27) *115	48 (Dall, 1891, p. 189)	Puget Sound to Panama Bay (Dall, 1908b, p. 364) Oregon to Panama (Dall, 1921, p. 9) 0° to 48° North Latitude [=Ecuador to Puget Sound] (Keen, 1937, p. 25)	60 to 1740 fathoms (Dall, 1908b p. 364) 1005 fathoms off California, type locality; 1740 fathoms off northern Ecuador (Woodring, 1938, p. 27)
15. *agassizi* Dall [1908, Harvard Coll. Mus. Comp. Zool., Bull., 43, pp. 365–66, pl. 16, fig. 10]	95 (Dall, 1908b, p. 365) *143 (Woodring, 1938, p. 27)	30	Tillamook Bay, Oregon to Aguja Point, Peru. (Dall, 1908b, p. 364) Gulf of California to Aguja Point, Peru. (Dall, 1908b, p. 365) 6° South Lat. to 46° North Lat. [=Aguja Point, Peru, to mouth of Columbia River, Oregon] (Keen, 1937, p. 25)	1036 to 1800 fathoms (Dall, 1908b, p. 364) 1588 to 1793 fathoms in Gulf of Panama; 1036 fathoms off Aguja Point, Peru. (Dall, 1908b, p. 365)
16. *bartschii* Dall [1908, Nautilus, 22, p. 61]	*191 (with periostracum 240 (Dall, 1908c, p. 62)	62.2 100)	"Albatross" stn. 5215 between islands of Ticao and Masbate, Philippines. (Dall, 1908c, p. 61)	600 fathoms (Dall, 1908c, p. 61)
17. *grandis* Verrill and Bush [1898, U. S. Nat. Mus., Proc. 20, p. 885, pl. 86, fig. 1, 2]	*42	22	"four stations between N. lat. 39° 58′ 30″, W. long. 70° 30′, and N. lat. 37° 24′, W. long. 74° 17′." (Verrill & Bush, 1898, p. 885). Off eastern coast of the United States between Chesapeake Bay and Nantucket. (Dall, 1908b, p. 364).	300 to 1600 fathoms (Verrill and Bush, 1898, p. 385)
18. *macrodactyla* Mabille & Rochebrune [1891, Miss. Sci. Cap. Horn, Zool., pt. 2 p. H109, pl. 8, fig. 4]	*62	22	Orange Harbor, Patagonia northward to Chiloë Isl., southwest Chile. (Dall, 1908b, p. 364)	20 to 369 fathoms (Dall, 1908b, p. 364)
19. *japonica* Dunker [1882, Index Moll. Mar., Japan, pp. 220, 261, pl. 14, fig. 3] Synonym: *yamakawai* Yokoyama [1927, Jour. Fac. Sci. Imp. Univ. Tokyo (2) 1, p. 435, pl. 50 figs. 10, 11] *fide* Habe, 1950, p. 62.	8.7 24 (Habe, 1950, p. 62)	3.0 10	Honshu, Japan	
20. *patagonica* Smith [1885, Sci. Res. Challenger, Zool., vol. 13, pp. 24, 208, pl. 11, fig. 1, 1a]	*38	18	West coast of South Patagonia, at Challenger Station 311, 52° 45′ 30″ S. lat. 73° 46′ W. long. (Smith, 1885, pp. 24, 208)	245 fathoms (Smith 1885, pp. 24, 208)
21. *prashadi* Vokes, new name [*grandis* Prashad 1932, Proc. Malac. Soc., London, 20 (3), p. 179, pl. 14, fig. 5]	*30	10	Laccadive Sea, "Investigator" station 260, 8° 28′ 15″ North lat., 76° 7′ East long. (Prashad, 1932, p. 179)	487 fathoms (Prashad, 1932 p. 179)
22. *tibai* Kuroda [1948, Jap. Jour. Malac., 15 (1–4, p. 29, text figs. 1–3]	*80	32.5	Off Cape Erima, Hokkaido, Japan. (Habe, 1950, p. 62)	
23. *winckworthi* Prashad [1932, Proc. Malac. Soc., London, 20 (3), p. 179, pl. 14, figs. 6, 7]	*15.2 27	4.8 8	Gulf of Manaar (between India and Ceylon)	3 fathoms (Prashad, 1932, p. 180)

from 60 fathoms in Puget Sound, 1005 fathoms off Lower California, and 1740 fathoms, near the Equator off northern Ecuador. The sole exception seems to be *S.* (*A.*) *winckworthi* Prashad, from 3 fathoms in southern India. The subgenus has been reported from the western Atlantic, eastern Pacific from Cape Horn to Puget Sound, western Pacific in Japanese and Philippine waters and in the Indian Ocean.

ADDITIONAL NOTES ON RECENT SPECIES

1. *Solemya parkinsoni* Gray is type, by original designation, of the "subgenus" *Zesolemya* Iredale 1939 (p. 232). The name may have some value, in a sectional sense, to include those species that have an internal rib "which divides into two to bound the [posterior] muscle scar." (See below, under discussion of *S. dalli* Clark.)

2. *Solemya terraereginae* Iredale and *S. velesiana* Iredale have both been referred by that author (1931, p. 201) to his "genus" *Solemyarina*. This was apparently originally erected only on the basis of the small size of these species and because the genotype was a Mediterranean species. Later (1939, p. 233) he added: "The small species I separated as *Solemyarina* show a rib formation and ligament structure more like that of the Neozelanic form [*S. parkinsoni*] than that of the large Australian shells [*S. australis* Lamarck]. The median rib is not curved, but is angulated posteriorly, while the anterior portion of the ligament is small and linear and the posterior portion is small and sublinear, the posterior muscle scar free." I have seen no specimens and cannot evaluate these characters; however, as indicated above, the name has not been adopted by subsequent authors.

3. *Solemya* (*Petrasma*) *occidentalis* Deshayes. Dall's (1908a, 1908b, p. 364) mention of a Mediterranean as well as western Atlantic distribution for this species has neither been accepted, nor commented upon, by subsequent authors and must be considered as requiring further confirmation. It is a small species with size measurements usually of the order of magnitude indicated above. Hence, Perry's (1940, p. 26) statement: "Alt. 9, length 25 mm." seems subject to question, being more applicable to *S.* (*P.*) *velum* Say.

The Upper Jurassic species, *Solen occidentalis* Stanton (1895, p. 55, pl. 10, figs. 2, 3), a homonym of the present form, is here renamed *S. stantoni* Vokes, new name. It was described from a limestone lense in the Knoxville "beds" 3.7 miles northwest of Paskenta, California. According to Anderson (1945, p. 961, pl. 5, fig. 3) it occurs in the lower part of the Newville group of the Knoxville series, and is of Tithonian age. He states: "The association of species collected from this lense is remarkable and seems to indicate a position near shore, though not on the strand line."

4. *Solemya* (*Acharax*) *johnsoni* Dall and *S.* (*A.*) *agassizi* Dall. Woodring (1938, p. 27) discusses the type and other material available to Dall when he described these species. He points out that the principle difference between the two was said to lie in the number of radial channels on the anterior portion of the valve, *S. agassizi* being said to have 6 or 7 anterior radial channels, as compared to 9 to 12 on *S. johnsoni*. He states:

> It appears doubtful whether two specimens are represented in the National Museum collections. All the specimens in the dried collection, representing localities from Oregon to Ecuador, are labelled *agassizi* in Dall's writing, or were so labelled under his direction. They have five or six grooves bordered by flat or slightly raised edges, but on some there is a transition from deep grooves to shallow grooves and ribs, and the number of grooves is a matter of judgment. . . . The specimens in the type lot of *johnsoni* have seven distinct grooves; those from station 3399 have seven to nine.

It should be pointed out that, if two species are represented, they were confused by Dall under the name *S. johnsoni*, and that therefore the geographic and bathymetric records given for that species prior to the description of *S. agassizi* in 1908 are not reliable.

5. *Solemya* (*Petrasma*) *pusilla* Gould and *S.* (*Acharax*) *japonica* Dunker. Dall (1908a, p. 2; 1908b, p. 364) states that *S. dunkeri* is the adult of the shell named *S. pusilla* Gould, and the latter name, having priority, is used, the species being assigned to the subgenus *Petrasma*. This conclusion has not been accepted by Japanese authors (see Habe, 1950, pp. 62, 63; 1951, pp. 17, 18) who assign the two to different subgenera, a procedure that has been followed here.

6. *Solemya* (*Acharax*) *prashadi* Vokes, new name. This species, based upon material

dredged by H. M. Indian Marine Survey Steamer "Investigator" was described as *Solemya* (*Acharax*) *grandis* by Prashad (1932, p. 179), and is a homonym of *S. grandis* Verrill and Bush (1898, p. 885, pl. 86, figs. 1, 2). The type specimen came from "Investigator" station 260, localized by Prashad as Laccadive Sea, 8° 28′ 15″ North latitude, 76° 7′ East longitude. It had been identified originally by E. A. Smith (1906, p. 253) with his *Solemya patagonica* (1885, p. 208) and said to be from "West of Cape Comorin, 487 fath., gray mud and Globigerina ooze." At the same time Smith also listed the species from "St. 327. W. of Burmah, 419 fath." stating: "A single specimen from the latter station is remarkable for its great size. The shell, exclusive of the extension of the periostracum is 100 mm. in length and 33 in height, . . . " Earlier, in 1895 (p. 11) he had reported the occurrence of his *S. patagonica* from "St. 151, off Colombo in 142–400 fathoms." And, in 1906 Melvill and Standen (p. 793) reported the presence in the Gulf of Oman, Lat. 24° 49′ N., Long. 56° 53′ East, at 225 fathoms, of a specimen whose identification with *S. patagonica* had been checked by Smith.

According to Prashad, only the specimen from Station 260 was available at the time he described his species; therefore only the data for that station are listed in the table. If the other specimens that were likewise identified as *S. patagonica* by Smith are conspecific with *S. prashadi*, the species attains dimensions more than three times that of the type specimen, its geographic range is extended to include most of the northern part of the Indian Ocean, and the bathymetric range is from 142 to 489 fathoms.

TERTIARY SPECIES

The writer's more or less casual search of the literature has revealed the following Tertiary fossil species and varieties that have been referred to the genus *Solemya*. In general the descriptions do not give sufficient information to permit subgeneric assignment of the species concerned.

Paleocene

1. *S. bilix* White (1881, U.S. Nat. Mus., Proc., 3, p. 158; 4, pp. 137, 139, pl. [unnumbered], fig. 9). This species, described by White from the Upper Cretaceous, Fox Hills sandstone or upper part of the Pierre shale near Golden, Colorado, has been reported as occurring in the upper part of the Cannonball formation by Stanton (1920, p. 19, pl. 1, figs. 1a, b). The specimens are said to range in length from 15 to 24 mm. The Midway, Paleocene, age of the Cannonball formation has been demonstrated by Fox and Ross (1942).

2. *S. hannonica* (Vincent) (1930, Mus. Roy. d'Hist. nat. Belg., Mem. 46, p. 63, pl. 3, fig. 1). This is a small generalized form from the "tuffeau de Ciply" of Belgium, referred to the Montian, Paleocene. The type is said to be 10.5 mm. long and 4 mm. in height; described as *Solenomya*.

3. *S. pavlowi* (d'Archiac). According to Vincent (1930, p. 64) "*Solecurtus? pavlowi* d'Archiac [is] une Solenomye incontestable." It was described from the "Paléocène volgien, étage inférieur de Syzron." The original reference has not been found.

Eocene

1. *S. blainvillei* Deshayes (1860, Desc. Anim. s. vert. du Bass. de Paris, 1, p. 732, pl. 15, figs. 15–17). A small species, said to be 7–8 mm. long and 3 mm. high, from the lower Eocene of the Paris Basin, France. Cossmann and Pissarro (1906, pl. 29, sp. 95–2) report it from the Cuisian stage.

2. *S. cuvieri* Deshayes (1860, sup. cit., p. 731, pl. 7, figs. 16–17). Length 31 mm., height 10 mm.; from the middle and upper Eocene of the Paris Basin, France. Cossmann and Pissarro (1906, pl. 29, sp. 95-1) report it from the Lutetian and Bartonian stages.

3. *S. angusta* (Deshayes) (1824, Desc. Coq. Foss. Env. Paris, I, Conch, p. 266, pl. 41, figs. 6–8; 1860, sup. cit., p. 732, pl. 15, figs. 12–14). A small species, originally described as a *Modiola*. It is from the middle and upper Eocene of the Paris Basin; Cossmann and Pissarro (1906, pl. 29, sp. 95-3) report it as a Lutetian and Bartonian species.

4. *S. subquadrata* (Foresti) (1879, Mem. Acad. Sci. d. Ist. Bologna (3) 6, p. 18 (126). Reported from the Eocene of Italy. The reference has not been seen; apparently described as *Solenomya gigantea* Mayer var. *subquadrata*, but Sacco (1901, p. 129) says it is a distinct species.

5. *S. insignifica* Eames (Philos. Trans.

Roy. Soc., London, 235B, no. 527, p. 328, pl. 10, fig. 30). A relatively small, (length 18.2 mm., height 8.0 mm.) and apparently well-named species from the Eocene of Western Punjab.

6. *S. alabamensis* Harris (1897, Bull Am. Paleontology, 2 (9), p. 265, pl. 20, fig. 12). The only Atlantic and Gulf coastal Tertiary species that I have noted. Described from the "Wood's Bluff Marl, 4 miles above Hamilton Bluff" on the Alabama River, it was later (Harris, 1919, p. 76) reported as from the "Sabine" stage from "St. Maurice; Ft. Gaines, Ga.; 5 miles N. of Orangeburg, S. C." and a specimen from the latter locality was figured (1919, pl. 26, fig. 16). The size mark given with the original illustration indicates a specimen 26 mm. long, and approximately 8 mm. high. The specimen from near Orangeburg, South Carolina, was said to be 31 mm. long.

7. *S. dunnensis* D. B. K. Palmer (1923, Univ. Calif. Publ. Geol. Sci., 14 (8), p. 302, pl. 55, fig. 1). The imperfect type specimen, 14.8 mm. long and 6.6 mm. high, was described as "*Solemya?*"; there seems no reason to doubt the generic assignment. The specimen came from the middle Eocene Vacaville shales of California. These are now generally referred to the Capay stage (Clark and Vokes, 1936).

8. *S.* sp., Clark and Woodford (1927, Univ. Calif. Publ. Geol. Sci., 17 (2), p. 85, pl. 14, fig. 1). A single, fragmentary specimen 29 mm. long (with the anterior end missing), and 16 mm. high, reported from the lower Eocene, Meganos formation, of California.

9. *S. lamarckiana* (Nyst & Le Hon) (1862, Desc. succinctes quelq. nouv. especies anim. et veg. foss. terr. eocenes env. de Bruxelles, p. 4). This reference has not been seen; Glibert (1933, p. 118) emends the specific name to *lamarcki* and lists several localities near Brussels, but gives no figure, or dimensions. Described as *Solenomya*.

10. *S. navicula* (Vincent) (1927, Ann. Soc. Roy. Zool. Malac., Brussels, 58, p. 44). A very small, smooth and glossy species ornamented only by weak growth lines. The type, from the upper Eocene "Sables de Wemmel," is 4.5 mm. long and 2 mm. high. Described as *Solenomya*.

11. *S. parvula* (Sowerby) (1822, p. 86, pl. 46, fig. 3). "There is found in the Calcaire Grossière, in the neighborhood of Valognes, a small species which we have named *S. parvula*, and represented in our plate; in its general form it approaches very nearly to the *S. mediterranea*, but it is notched at the umbo, a character in which it resembles the *S. australis*, which, however, we have never seen. We therefore decline giving a specific character of *S. parvula*." This Paris Basin Eocene species has apparently been generally overlooked by subsequent authors although Deshayes (1857, p. 139) in the discussion accompanying his description of *S. occidentalis* makes the following totally unfounded observation regarding the species: "*parvula* Sow. Espece douteuse, figurée par Sowerby dans le Genera of Shells, mais d'une manière insuffisante. Point de description. Aucune indication de localité."

Oligocene

1. *S. dalli* Clark (Univ. Calif. Publ. Geol. Sci., 15 (1) p. 73, pl. 22, fig. 3). This is a relatively large species, the holotype being 55 mm. long and 17 mm. high; specimens in the writer's collections from the Keasey formation of Oregon show lengths up to 76.2 mm. and heights to 23.7 mm. Tegland (1933, pp. 103–104, pl. 4, figs. 1–10) has given excellent illustrations of topotype specimens. Concerning one of these she stated: "A fortunately well preserved specimen . . . shows the ligament to be external, paravincular and opisthodetic, characteristics of the subgenus *Acharax*." Preparation of an interior of a Keasey specimen by the writer shows that there was also a considerable amount of the ligament that was internal and amphidetic in position, indicating its reference to *Solemya* s.s. of Dall's classification. There is also an internal rib supporting the "chondrophore" and bounding the posterior adductor, that is identical in character to that described by Iredale (1939, p. 233) for the Recent *S. parkinsonii* Gray. This species is the type of his *Zesolemya*, a term which may prove useful in a sectional sense for these large *Solemya* s.s. There is no internal rib present in *Acharax*. *S. dalli* appears to range throughout the Oligocene of northwestern Oregon and of Washington, but has not as yet been reported from California.

2. *S.* (*Acharax*) *willapaensis* Weaver

(1943, Washington Univ. (Seattle) Publ. Geol., 5, p. 21, pl. 6, figs. 2, 17). The holotype of this species was originally figured by Tegland (1933, pp. 102–3, pl. 4, fig. 12) as *S. (Acharax) ventricosa* Conrad, a Miocene species. It came from strata of Keasey, lower Oligocene, age on the Willapa River, near Holcomb, Washington. A single specimen has been identified from the type area of the Keasey formation in northwestern Oregon. The type specimen is 87 mm. long and 39 mm. high, being distinctly higher in proportion to its length than is *S. dalli*, with the umbones also more central in position. The specimen from the Keasey formation shows no trace of an internal rib, and the assignment to the subgenus *Acharax* is provisionally accepted.

3. *"S. (Acharax)" belenensis* Olsson (1931, Bull. Am. Paleontology, 17 (63), p. 127 (31), pl. 3, fig. 7). Described from the Heath formation, upper Oligocene, of Peru, this species is distinguished by its very weak radial ribbing, being almost smooth externally. The holotype is 84 mm. long and 25 mm. high.

4. *"S. (Solemya)" lomitensis* Olsson (1931, Bull. Am. Paleontology, 17 (63), p. 127 (31), pl. 3, fig. 5). Described from the Oligocene (?) Lomitos cherts of Peru, this species is based on internal molds that show faint impressions of radial ribs and traces of periostracal digitations, confirming the generic assignment. On the holotype the posterior area is broken away, and neither the figure nor the description gives information as to the nature of the hinge and ligamental area. Length 60 mm. (estimated to have been about 70 mm.), height 28 mm.

5. *S. obovata* von Koenen (1868, Palaeontographica, 16, p. 242, pl. 28, figs. 5a–d). Described as from the middle Oligocene at Hermsdorf, Germany, this species is apparently marked by having relatively strong growth lines and weak radial ribbing. The type is 10 mm. long and 4.5 mm. high. Vincent (1927, p. 44) mentions that he has determined the species from the "argile de Boom" Belgium.

6. *S. haeringensis* Dreger (1904, Jahrb. k. k. Geol. Reichsanstalt., 53, H. 2, p. 268, pl. 12, fig. 4). Described from the Lattorfian, Oligocene, at Häring, in the Tyrol, the species has five radial ribs on the anterior portion of the valve; three of these, reaching the anterior end, are separated by distinct furrows. Over the rest of the shell the radial ornamentation is poorly developed, marked by weak nodes where crossed by the strong growth lines. Dimensions are not given, but the figure, said to be natural size, is 24.4 mm. long and 8 mm. high at the umbo.

Miocene

1. *S. döderleini* (Mayer) (1861, Jour. de Conchyl., 9, p. 364). This species seems to be very widely distributed throughout the European Miocene. Davies (1935, p. 193) lists it as from the middle Miocene " 'Schlier' (between 1st and 2nd Mediterranean stages) Vienna B. and large parts of Mediterranean area; also Mio. Denmark." It has been well figured by Sacco (1901, p. 128, pl. 27, figs. 1–4), who states that the size ranges from 25 to 90 mm. in length and 9 to 30 mm. in height. However, he considers *S. gigantea* Mayer as a variety of *S. döderleini* and refigures Mayer's original illustration of that species; this has the larger dimensions given by Sacco. The largest specimen figured by Sacco as *S. döderleini* s.s. measures, on the illustration, 64 mm. in length and 20 in height. No data as to the nature of the interior and ligamental area is available, but the exterior has much the aspect of species referred to *Acharax*. Described as *Solenomya*.

2. *S. döderleini* var. *latesulcata* Sacco (1901, I Moll. terr. Terz. del Piemonte e del Liguria, pt. 29, p. 129, pl. 27, fig. 6). The type, from the Miocene of Italy, measures, on the original figure, 71 mm. in length and 25 mm. in height. Described as *Solenomya*.

3. *S. döderleini* var. *colligens* Sacco (1901, p. 129). In his discussion of *S. döderleini* Sacco makes the following statement: "La figura datta dall'Hoernes [1862, p. 257, pl. 34, figs. 10a, b] sopra un esemplare di Vöslau non corresponde alla forma typica torinese ma tende spiccatamente verso la *S. togata* per modo che ne farei una var. *colligens* Sacco." The specimen in question was stated by Hoernes to be 45 mm. long and 15 mm. high.

4. *S. gigantea* (Mayer) (1868, Jour. de Conchyl., 16 p. 102, pl. 2, fig. 1). The largest of the European species, considered a variety of *S. döderleini* by Sacco (1901, p. 129, pl. 27, fig. 5). In the description Mayer

indicates the dimensions of the type as length 85 mm. height 33 mm. The rather diagrammatic figure is slightly longer in proportion to the height of the shell.

5. *S.* (*Acharax*) *ventricosa* Conrad (1849, Geol. U.S. Expl. Exped. p. 723, pl. 17, figs. 7, 8). This species, based upon two specimens collected by Dana from strata now referred to the middle Miocene Astoria formation at Astoria, Oregon, was inadequately described and poorly figured by Conrad. Weaver (1943, pp. 18–9, pl. 5, figs. 1–3) has refigured Conrad's type specimens, and an additional specimen from the same area and gives a number of valuable observations on the species. He has indicated that the original of Conrad's plate 17, figure 7, is the holotype. According to Conrad the species had a length of 3¾ inches and a "breadth" of 1½ inches; Weaver gives no specific measurements, but does state that the height is 33 percent of the length of the shell. According to Dall (1909, p. 101) *Donax ? protexta* Conrad (1849, sup. cit., p. 723, pl. 17, fig. 9), also described from Astoria, was "based on an imperfect internal cast of a young specimen of *Solemya*, doubtless the same species as the larger and better-preserved specimens obtained simultaneously at the same locality." Woodring (1938, p. 28) concurs.

6. *S.* (*Acharax*) *burica* Olsson (1942, Bull. Am. Paleontology, 27 (106), p. 23, pl. 2, fig. 1). A fragment 58 mm. long and 47 mm. high, described from the Burica formation, uppermost Miocene or lower Pliocene age, of Panama and Costa Rica; when complete, the specimen is estimated to have been approximately 115 mm. in length.

7. *S.* (*Acharax*) *tokunagai* Yokoyama (1925, Jour. Coll. Sci., Imp. Univ. Tokyo, 45 (5), p. 31, pl. 6, figs. 1–3). Described as from the Shirado Series, Pliocene, of the Joban coalfield, Honshu, Japan, from strata that are presently referred to the Kamenoo, Mizunoya and Honya formations, approximately middle Miocene in age (Hatai and Nisiyama, 1952, p. 135). The original of Yokoyama's figure 2, from the Kamenoo formation has been selected as the holotype (Hatai and Nisiyama, 1952, p. 135); its dimensions are according to Yokoyama, length 94 mm. and height 38 mm., but these figures clearly include the well-preserved periostracal prolongations. The shell itself, so far as can be determined from the original illustration is 81 mm. long and 28 mm. high at the umbones. Kanehara (1937, p. 156, pl. 15, fig. 10) has figured a topotype from the Kamenoo formation and (figure 11) a specimen from the upper Miocene-lower Pliocene Oiwake formation of Hokkaido that he has identified as this species. So far as can be determined from the illustration this specimen is not conspecific with those from the middle Miocene. The anterior ornamentation of *S. tokunagai* consists of relatively narrow ribs separated by interspaces that are as wide or are wider than the ribs and are plane, without any secondary inter-ribbing being developed in them. Furthermore, especially on the holotype, these anterior ribs show a marked ventral curvature. The upper Miocene specimen figured by Kanehara has proportionately wider ribs with well-developed secondary riblets in the interspaces; the ribs are straight, with no trace of any ventral curvature. In many respects, this specimen resembles *S. dalli* Clark in the details of its ornamentation.

8. *S.* (*Acharax*) *yessoensis* Kanehara (1937, Jap. Jour. Geol. Geogr., 14 (3–4) p. 155, pl. 15, fig. 12). This species, from the upper Miocene portion of the Oiwake formation of Hokkaido, has the broad interspaces of *S. tokunagai* but differs entirely in the shape of the anterior end, and in its more elongate, narrower posterior end of the valve. The holotype is said to be 84 mm. long and 26 mm. high.

9. *S.* n. sp. Marwick (1931, Geol. Surv. New Zealand, Pal. Bull. 13, p. 48, pl. 1, fig. 1). Large casts of an undescribed species of *Solemya* from the Tutamoe series, Awamoan stage, lower Miocene of the Gisborne district, North Island, New Zealand, represent according to Marwick, the first record of the genus from the Tertiary of New Zealand. One of the casts is said to be "25×70 mm."

Pliocene

1. *S.* (*Petrasma*) *labeosa* Yokoyama (1928, Jour. Fac. Sci., Imp. Univ. Tokyo, (2) 2, pl. 68, fig. 11). Based upon a single worn specimen, 24 mm. long and 8.6 mm. high, from the Pliocene deposits of the oil field at Higashiyama, Echigo Province, Japan. Re-

ferred to the subgenus *Petrasma* by Hatai and Nisiyama (1952, p. 135).

2. *S. togata* (Poli) [see table of Recent species]. In a tabular presentation of the distribution of the species of *Solemya* in the Italian Tertiary, Sacco (1901, p. 129) lists this species as present in the Pliocene, giving no locality or other information.

3. *S.* (*Acharax*) aff. *S.* (*A.*) *johnsoni* Dall, Woodring, 1938, U. S. Geol. Survey, Prof. Pap. 190, p. 27). A single specimen, consisting of the greater part of a paired gaping shell, restored length about 45 mm., height 15.8 mm., from the Repetto formation, lower Pliocene, of the Los Angeles Basin, California, obtained from the core of Standard Oil Co. Baldwin No. 73 well, in the Montebello Field, at a depth of 3,340 to 3,358 feet.

4. *S.* (*Acharax*) *ventricosa* Conrad [see Miocene species]. Martin (1916, pp. 238, 240, 254) has listed this species as occurring in the fauna of the upper Miocene or lower Pliocene beds exposed at the mouth of Bear River, near Cape Mendocino, California, and in the lower strata of the Wildcat formation, Pliocene, of Humbolt County, California. No description or illustrations are given.

Pleistocene

1. *S. yamakawai* Yokoyama (1927, Jour. Fac. Sci., Imp. Univ. Tokyo, (2) 1, pt. 10, p. 435, pl. 50, figs. 10, 11). This species, based on specimens from the Pleistocene deposits of Ōji, near Tokyo, is said by Habe (1950, p. 62) to be a synonym of *S.* (*Acharax*) *japonica* Dunker. The type is 12 mm. long, 3 mm. high; another specimen, a left valve, is said to be "about 16 mm. long . . . 5.8 mm. high." In the faunal list "giving the names of all the species determined" Yokoyama (1927, p. 403) lists a "*Solemya dunkeri* Yok." with the locality Kurumachō. I have been unable to find a description, or other reference to such a form. Since the list does not mention *S. yamakawai*, it is possible that both the name and the locality indicated in the list are the result of a lapsus.

Genus ADULOMYA Kuroda in Homma 1931

Audulomya KURODA in Homma, 1931, Nagano nat. Hist. Soc., no. 4, p. 27.

Type species, by monotypy?: *Adulomya uchimuraensis* Kuroda in Homma.

I have not been able to see the original description of this genus. It is referred to the family *Solemyacidae* on the authority of Habe (1950, p. 17), and Nomura (1935, p. 30) described a species as *Solemya* (*Adulomya?*) *hachiyai* that is referred by Hatai and Nisiyama (1952, p. 134) to *Adulomya* as a genus.

Judging from the description of Nomura, the genus is based upon very large shells of solemyacid outline that lack radial ornamentation, and tend to possess a small ventral gape, as well as the usual anterior and posterior ones.

The following three described species are all from strata of Miocene age in Japan:

1. *A. uchimuraensis* Kuroda in Homma (1931, Nagano nat. Hist. Soc. 4, p. 27, pl. 13, figs. 111–114). According to Nomura (1935, p. 31) *A. uchimuraensis* is "somewhat related to" *A. hachiyai* Nomura "in general aspects, but is easily distinguished from that species in being much larger and having proportionately deeper and higher valves. Kuroda's species, as a whole, is more slender and linear than the present new species." The context is not clear, but apparently *A. uchimuraensis* is considerably smaller than the 190 mm. length given from *A. hachiyai*.

2. *A. chitanii* Kanehara (1937, Bull. Imper. Geol. Surv., Japan, 27 (1), p. 19, pl. 5, figs. 1, 6–9).

3. *A hachiyai* (Nomura) (1935, Saito Ho-on Kai Mus., Res. Bull. 6, p. 30, pl. 6, fig. 5, pl. 7, figs. 1, 2). Measurements of two specimens give lengths of 190 mm. and heights of 50 mm.; a third is 180 mm. long and 46 mm. high.

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JOURNAL OF PALEONTOLOGY, VOL. 29, NO. 3, PP. 546–551, 2 TEXT-FIGS., MAY 1955

PALEONTOLOGICAL NOTES

MORE SCORPIONID TRACKWAYS FROM THE PERMIAN LYONS SANDSTONE, COLORADO

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Toepelman and Rodeck (1936) identified a fossil trackway collected in the vicinity of Boulder, Colorado, as *Paleohelcura?* Gilmore, 1926, and described it as a new species, *P.? lyonsensis*. A study of the range of variation of similar fossil and Recent trackways (Brady, 1947) indicates that the Lyons specimen could be considered as a normal variant of *P. tridactyla* Gilmore, 1926, or of the category of ichnites described by Faul and Roberts (1951, p. 272) as F 8.1.

The trackway described by Toepelman and Rodeck is preserved on a sandstone slab for which they had no locality data. Their conclusion, based on lithologic similarity, that the slab had come from some (admittedly unknown) horizon in the Lyons sandstone can now be supported. In July, 1954, numerous trackways of invertebrates were found in place in the Lyons sandstone by members of the University of Michigan Geology Summer Field Camp staff. The locality is a road cut about one-quarter mile northwest of the entrance to the Lazy J S ranch about 3.6 miles north northwest of Boulder in the S.W.$\frac{1}{4}$, S.E.$\frac{1}{4}$, N.E.$\frac{1}{4}$, Sec. 11, T. 1 N., R. 71 W., Boulder Co., Colorado (see sketch map). Minor folding and extreme crossbedding of the Lyons sandstone make the exact stratigraphic horizon of these trackways uncertain, but without much doubt they occur within the upper one quarter of that formation. The trackways, all of the same general character, crisscross an area of outcrop about 8 by 10 feet square. With little doubt all may be assigned to the scorpionid, *Paleohelcura tridactyla* (Gilmore, 1926, emended by Brady, 1947, p. 468) or to the ichnites category F 8.1 of Faul and Roberts (1951, p. 272).

The trackway patterns commonly consist of two parallel lines of footprints, the individual prints arranged in triangular clusters of three, the clusters alternating on the two sides of the trail, an apex of each triangular

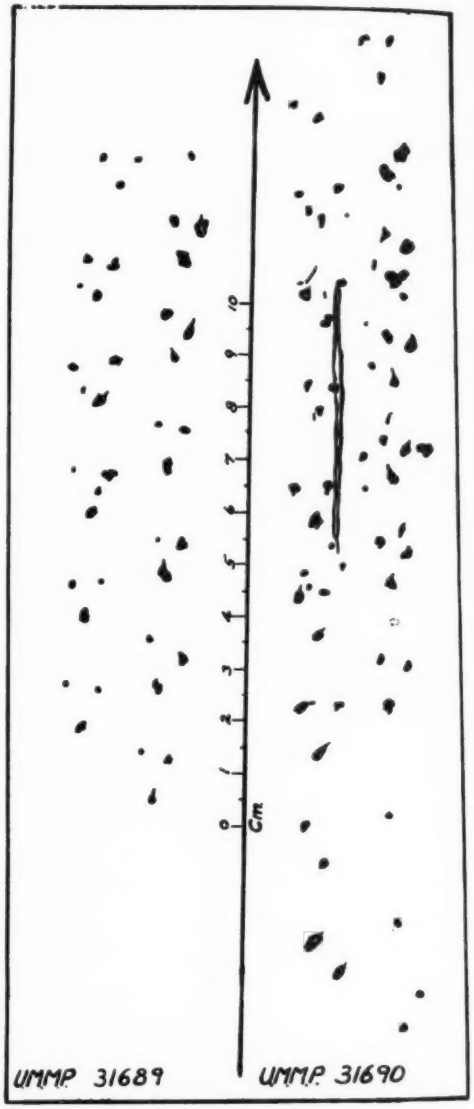

FIG. 1—*Paleohelcura tridactyla* trackways from the Lyons sandstone. University of Michigan, Museum of Paleontology catalogue specimens. Centimeters for scale.

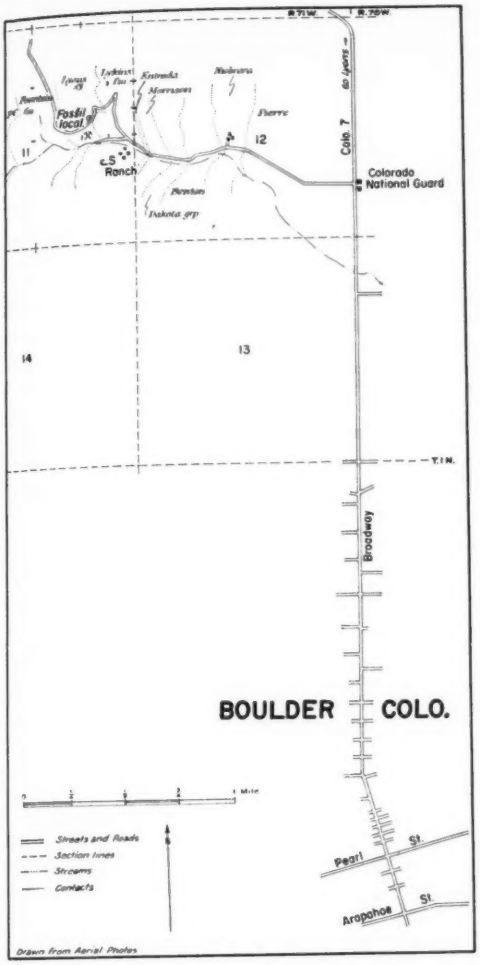

FIG. 2—Sketch map showing location of the outcrop of Lyons sandstone bearing the scorpionid trackways.

cluster directed rearward. There are imprints of a fourth foot in some clusters, and occasional short, discontinuous tail drags. The individual footprints usually are shallow pits of irregular outline but occasionally show the linear stroke of a single claw at the forward edge of the pit, and/or a low mound of sand pushed up behind. The average width of the trackways figured here is 24.5 mm. The clusters of prints fall within circles whose average diameter is 10.7 mm. The average distance between the posterior apices of successive clusters in any one line of prints is 20.5 mm. Two small blocks, University of Michigan, Museum of Paleontology Numbers 31689 and 31690, were removed from the exposure but the majority of the trackways remain in place.

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CORRECTION

In a note entitled "O tempora, o mores" by Otto H. Haas, which appeared in the January 1955 issue of this journal, the generic name in the title of Dr. Jillson's paper is misquoted *Brachiosponga*, instead of *Brachiopongia*.

STRATIGRAPHIC AND GEOGRAPHIC RANGE OF THE LATE CRETACEOUS PELECYPOD *DIDYMOTIS*[1]

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ABSTRACT—The pelecypod *Didymotis* had a narrow stratigraphic range and a very wide geographic range just prior to the middle of the Late Cretaceous. Its unusual combination of characteristics should make easy its recognition by field geologists.

The recent comments by Rutsch and Salvador (1954, pp. 423, 424) concerning the Cretaceous pelecypod *Didymotis* in South America indicate that most Mesozoic stratigraphers are not aware that this genus has a narrow stratigraphic range and a wide geographic range. Its potential usefulness as a Late Cretaceous marker may be shown by presenting its characteristics and occurrences on several continents.

The generic characteristics of *Didymotis* listed by Gerhardt (1897, pp. 180, 181) were prepared for comparison with such genera as *Posidonia*, *Monotis*, and *Daonella* and may be summarized as follows: shell paper thin, elongate, equivalved; beaks inclined forward, not prominent; anterior and posterior ears present, the posterior ear the larger; no byssus present; hinge line long and straight; sculpture consisting of concentric growth lines and folds, with or without radial ribs on the middle third of the shell.

This definition needs qualifying in regard to the ears. Rutsch and Salvador (1954, p. 424) mention that the specimens of *Didymotis* from South America that they examined do not show ears. Among the 34 specimens available to the writer there is no trace of an anterior ear, but there is an elongate depressed area that is posterior to the beaks and that in some specimens is separated by a weak groove from the remainder of the shell. This depressed area is crossed by the concentric ribbing of the shell and is much less earlike than the anterior ear of the Triassic *Halobia*.

In South America *Didymotis* has been found with ammonites in Trinidad, Venezuela, and Colombia. In Colombia *D. variabilis* Gerhardt has been found with *Barroisiceras rhombiferum* (Gerhardt) (1897, see fossil list opposite p. 122). *D. roemeri* (Karsten) has been found with *Prionocycloceras guayabanum* (Steinmann) (Gerhardt, 1897, p. 123) and *Gauthiericeras margae* Schlüter (Fritzsche, 1924, p. 332). In Venezuela *D. variabilis* has been found with *Peroniceras* and *Barroisiceras* (Sutton, 1946, p. 1650). In Trinidad cores from the Trinidad Leaseholds Ltd. Morne Diablo Well no. 34, located Lat. 10°07′30″ N., Long. 61°25′15″ W., contained *Didymotis trinidadensis* Sommermeier from the depths of 12,834 to 13,274 feet, *Didymotis variabilis* Gerhardt from the depth of 13,281 feet, and *Barroisiceras* from the depths of 13,260 to 13,346 feet. The lower Turonian pelecypod *Inoceramus labiatus* Schlotheim occurred at the depths of 13,458 to 13,481 feet. In Trinidad, also, *Didymotis trinidadensis* Sommermeier has been found with *Barroisiceras* at the Hermitage Quarry in Union Village north of Pointe-à-Pierre.

Concerning the above ammonites, such genera as *Barroisiceras*, *Prionocycloceras*, and *Gauthiericeras* are considered excellent evidence for an early Coniacian age. In North America *Barroisiceras* occurs directly above the late Turonian *Prionocyclus* and is never associated with it. In South America, however, there are several records of *Barroisiceras* associated with *Prionocyclus* or even earlier Turonian genera such as *Thomasites*, *Mammites*, and *Hoplitoides*. These unusual associations might be explained by collecting difficulties, by failure to collect zonally, or by longer ranges of certain genera in South America than elsewhere. Regardless of the explanation, it is significant that *Didymotis* has never been recorded in South America with typical Turonian ammonites, and at a number of places it has been recorded with early Coniacian ammonites.

[1] Publication authorized by the director, U. S. Geological Survey.

In southern Mexico many well-preserved specimens of *Didymotis trinidadensis* Sommermeier have been found associated with early Coniacian ammonites by Carl Fries, Jr., of the U. S. Geological Survey. The species was found with *Barroisiceras* and *Otoscaphites* in the Chinameca Canyon 3 kilometers downstream from La Era, Morelos; with *Peroniceras* at Nexpa in the Chinameca Canyon, Morelos; with *Peroniceras* and *Otoscaphites* at Zumpango del Rio, Guerrero. Specimens of *Didymotis* from Zumpango del Rio were described by Böse (1923, pp. 190, 208–210, pl. 17, figs. 19, 20) as species of *Inoceramus*. These had been collected by Burckhardt (1919, pp. 122–124, chart opposite p. 130; 1930, pp. 236–239) along with the ammonites *Otoscaphites* and *Barroisiceras*. Burckhardt considered that the presence of small scaphitids with lateral lappets (*Otoscaphites;* Wright, 1953) indicated a late Turonian age in spite of the associated *Barroisiceras*, which was not known below the Coniacian; but now such scaphitids have been found in the Coniacian in various parts of the world (Wright, 1953).

In northern Mexico a typical specimen of *Didymotis* was found by Teodoro Diaz, of Petróleos Mexicanos, from 100 meters of limestone and shale that forms the top of the eastward dipping escarpment of the Sierra del Carmen, about 55 kilometers S. 55°E. of Boquillas in northern Coahuila. This specimen was associated with species of *Inoceramus* comparable with *I. subquadratus* Schlüter and *I. mytilopsis* Conrad, which are characteristic of the Austin chalk of Texas. As the Austin chalk is of Coniacian to Santonian age, the occurrence of *Didymotis* in northern Coahuila should belong within the same time span.

In Japan the genus *Didymotis* is probably represented by specimens referred to *Inoceramus* (*Sergipia?*) *akamatsui* Yehara (Nagao and Matumoto, 1940, pp. 54, 55, pl. 13, figs. 3, 5, pl. 22, fig. 6). This species occurs most commonly associated with *Inoceramus uwajimensis* Yehara and with various species of the ammonites *Parapuzosia*, *Damesites*, *Nowakites*, and *Prohauericeras* that are excellent evidence of a Coniacian age, but there are some records of *I. akamatsui* from older beds of Turonian age (Matumoto, 1942, pp. 134, 147–149; Matsumoto et al., 1953, p. 19). It is interesting that Nagao and Matumoto (1940, p. 55) noted the remarkable resemblance of *I. akamatsui* Yehara to the specimens of *Didymotis* from southern Mexico described by Böse (1923, pp. 208–210) as *Inoceramus*. They also noted that the Japanese species reminded them of "some forms of *Posidonomya*" which is essentially what Gerhardt (1897, p. 179) said concerning the type of the genus, *Didymotis variabilis* Gerhardt. Perhaps the fact that *Posidonia* is not known above the Jurassic influenced the assignments to *Inoceramus* made by Böse and the Japanese paleontologists.

Judging from the specimens in hand, *Didymotis* differs from *Inoceramus* by having a paper-thin shell, inconspicuous subcentral beaks, a depressed area posterior to the beaks, somewhat crinkled ribbing, and by lacking ligamental pits on the hinge. It differs from *Posidonia* by having a more elongate shape, a longer hinge line, radial ribs, and a depressed area posterior to the beaks.

In summation, *Didymotis* partakes of some of the characteristics of both *Inoceramus* and *Posidonia* and has been confused with them. It usually occurs in shaly rocks associated with ammonites and *Inoceramus*. It occurs in greatest abundance in rocks of early Coniacian age, but there are records from Japan of some occurrences in rocks of Turonian age. Its unusual combination of characteristics and its rather restricted stratigraphic range should make it a very useful fossil for the field man. Its wide distribution from South America to Japan suggests that it has a world wide distribution and is probably represented in many museum and university collections under other names than *Didymotis*. For example, the European species of *Inoceramus* mentioned by Böse (1923, p. 209) should be reexamined as possible European representatives.

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ARTHROPHYCUS ALLEGHANIENSIS AS A GUIDE FOSSIL IN NORTHERN VIRGINIA[1]

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ABSTRACT—*Arthrophycus alleghaniensis*, common in the Clinch-Tuscarora sandstone (Albion) of Virginia, is reported for the first time from the Keefer sandstone (Niagaran).

The primary purpose of this note is to report an apparently new stratigraphic occurrence of *Arthrophycus alleghaniensis* (Harlan). The physical characteristics and problematical status of this form are familiar to most Appalachian geologists and will not be reviewed here. It will suffice to state that *A. alleghaniensis* is one of the more easily recognized fossils of the Paleozoic.

In the course of routine field mapping of the Edinburg, Virginia-West Virginia quadrangle, for the Virginia Geological Survey, "worm trails" identical with *A. alleghaniensis* (Fig. 1) were observed in the Keefer sandstone (mid-Niagaran) at two localities. Both of these localities are along roads on the east side of Tibbets Knob on Great North Mountain. In this area, the Keefer consists of 60 to 70 feet of orthoquartzite with subordinate green and purple shales. *Arthrophycus* is found in the middle portion of the unit.

[1] Published with permission of the State Geologist of Virginia.

Locality 1: West side of state secondary highway 779, 4.5 miles N. 53°W. of Columbia Furnace, Shenandoah County, Virginia; elevation 1908 feet. This is best exposed and most accessible outcrop of middle Keefer with *A. alleghaniensis*.

Locality 2: North side of state secondary highway 781 (also state route 59), 4.5 miles N. 69°W. of Columbia Furnace; elevation 1840 feet. The fossils are less abundant and less well preserved than at locality 1.

As well as can be determined, previously reported occurrences of *Arthrophycus* in Virginia and West Virginia have been confined to the Clinch-Tuscarora sandstone, of Albion age, and the Massanutten sandstone, the age of which is not precisely known.

As for the Keefer, Butts (1940, p. 246) states that "no fossils have been observed in the sandstone beds in Virginia, but *Scolithus* tubes occur locally in them in Maryland." Woodward (1941, p. 92) reports that *Scolithus keeferi* is fairly common in West Virginia.

In spite of its apparent restriction to beds

FIG. 1—*Arthrophycus alleghaniensis* (Harlan) from the mid-Niagaran Keefer sandstone, locality 1. Note the characteristic annulations below the knife. Knife is 3 inches long.

of Medinan age in Maryland, West Virginia, and Virginia, Woodward, in 1941, stated that "the reliability of *Arthrophycus alleghaniensis* as a guide fossil is now open to question, as it haunts the Oneida and higher Clinton members of New York. Probably it should no longer be considered a necessary index of Medinan age." The Keefer occurrence of *A. alleghaniensis* supports the above statement. It would seem that this form is a facies fossil restricted to the clean sandstones of Albion and lower Niagaran times. The index value of *A. alleghaniensis* is thus either greatly reduced or completely nullified by this stratigraphic extension.

With this new occurrence, *Arthrophycus* is now known from three formations in northern Virginia: The Tuscarora, Massanutten, and Keefer. The lithologies of these units are remarkably similar; all are orthoquartzites with minor local shales. The Tuscarora and Keefer have been correlated rather precisely with Silurian sections elsewhere, but the exact age of the Massanutten is not known.

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At Edinburg Gap, in Shenandoah County, the Massanutten overlies Martinsburg sandstone and is overlain by red beds. The red beds are divided by a thin persistent white sandstone. In the absence of delimiting fossil zones, questions arise involving (a) the time span covered by the Massanutten sandstones, and (b) the age of the overlying red beds. There seems no doubt that the Tuscarora is represented in Massanutten Mountain, but there are three possibilities concerning the Clinton: (1) it is not represented in the section, (2) it is present as the upper portion of the 800 feet of orthoquartzites, or (3) it is present as the lower portion of the red beds overlying the orthoquartzites. Swartz (1938, p. 27) advanced the last interpretation. However, because of (1) the presence of *Arthrophycus* throughout the Massanutten, (2) the nearly homogeneous nature of the Massanutten quartzites, (3) the absence of Clinton lithology and fossils, and (4) the presence of typical Bloomsburg lithology above the Massanutten, it is here assumed that the basal Silurian sandstones thicken rapidly from the Great North Mountain area toward the east. The Clinton in its *typical* development is absent in Massanutten Mountain. This is not to infer that the Clinton equivalent is absent, for the thick beach deposits of the Massanutten must transgress time planes. It is therefore suggested that the Clinton is represented by the upper 300 to 500 feet of the Massanutten sandstone. Thus, the Massanutten formation occupies the Albion and half of the Niagaran intervals, the same time span apparently occupied by *A. alleghaniensis*.

The aid of Raymond S. Edmundson of the Department of Geology, University of Virginia, in verifying the stratigraphic horizon, and C. Coleman Fisher, Division of Geology, Charlottesville, Virginia, in editorial criticism, is gratefully acknowledged.

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NOMENCLATURAL NOTES

NOMENCLATURAL REVIEW OF THE PALEOZOIC PELECYPOD FAMILY CONOCARDIIDAE

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ABSTRACT—The nomenclaturally acceptable genera and subgenera of conocardiids are as follows: *Conocardiopsis* Beushausen, 1895; *Conocardium* Bronn, 1834; *Hippocardia* Brown, 1843; *Rhipidocardium* Fischer, 1887.

The conocardiids are an aberrant family of Paleozoic pelecypods which are greatly in need of taxonomic revision. This paper is a preliminary study concerning only the previously proposed genera and subgenera of the family and their type species. For a good description of *Conocardium*, sensu lato, see La Rocque (1950, pp. 317–318).

The following genera and subgenera are conocardiids with type species having morphological characters that correspond to those of the family and names that are nomenclaturally valid. This does not mean that all will be acceptable when careful work on the classification of the Conocardiidae is completed, but these names form a basis for future taxonomic work on the family.

Conocardiopsis Beushausen, 1895, pp. 378–379. Type species (monotypy) *Cardium lyellii* d'Archiac and de Verneuil, 1842; Middle Devonian; Germany. Figured, Beushausen, 1895, pl. 28, fig. 14.

Conocardium Bronn, 1834, p. 92. Type species (monotypy) *Cardium elongatum* Sowerby, 1815; Mississippian; Derbyshire, England. Figured, Sowerby 1815, vol. 1, pl. 82, fig. 3.

Hippocardia Brown, 1843, p. 97. Type species (original designation) *Cardium hibericum* Sowerby, 1815; Mississippian; vicinity of Cork, Ireland. Figured, Sowerby, 1815, vol. 1, pl. 82, figs. 1–2.

Rhipidocardium Fischer, 1887, p. 1036. Type species (monotypy) *Conocardium amygdala* Barrande, 1881; Devonian; Czechoslovakia. Figured, Barrande, 1881, Ordre des Acéphalés, vol. 4, pl. 201, fig. II (1–2). The original figures are so poor that there is some doubt that they represent a conocardiid.

The following names are rejected from the family Conocardiidae. They include homonyms, names referable to other families, names by non-binomial authors, and misspellings. The names listed by Paetel have been ignored because he has so compounded errors that his work is practically useless.

Arcites W. Martin, 1809, pl. 44. Martin's names published under the title *Petrificata Derbiensia* have been rejected for nomenclatorial purposes. See Opinion 231.

Bilobite and *Bilobites* Dekay, 1824, pp. 45–49, pl. 5. These names are not used in a generic sense. For a good review of the problem, see Sinclair (1951, pp. 229–230).

Euchasma Billings, 1865, pp. 200, 360–361. Type species (monotypy) *Conocardium blumenbachii* Billings, 1859; Lower Ordovician; Newfoundland. *Euchasma* has been placed in the Crustacea by some paleontologists, but its outline and radial ribs give it the appearance of a bivalve mollusk related to the conocardiids.

Goldfussia Castlenau, 1843, p. 43. Not a conocardiid.

Lichas Steininger, 1837, p. 231. Type species (monotypy) *Lichas antiquus* Steininger, 1837; homonym of *Lichas* Dalman, 1827.

Pleurorhynchus Phillips, 1836, pp. 210–211. Homonym of *Pleurorhynchus* Rudolphi, 1801, emendation for *Pleurorinchus* Nau, 1787.

Pleyrorhynchus Eichwald, 1860, p. 1021. Error for *Pleurorhynchus* Phillips, 1836.

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NOTES ON THE TAXONOMY OF THE BRANCHIOPODA NOTOSTRACA

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ABSTRACT—The genera which have been assigned to the Notostraca are briefly reviewed. It is concluded that the only valid genera of this order are *Apus* and *Lepidurus*.

In preparing the section on the Branchiopoda for the Treatise, various taxonomic tangles have been encountered. Since no place is afforded in the Treatise for the author's evidence or arguments in making reassignments, those pertaining to the unit on notostracans are discussed here.

PARATRIOPSIDAE AND TRIOPSIDAE

Tchernyshev (1940) set up two new families assigned to the tribe (=order) Notostraca: Family I, Paratriopsidae; Family II, Triopsidae. Family I included two new Jurassic genera from Turkestan, namely, *Ketmenia* and *Iliella*. In addition, the author assigned *Protocaris* Walcott to this family. He noted that *Protocaris marshi* Walcott "may be considered as the nearest to them" (i.e., the above-named new genera). Further, the observation was made that the new genera differ considerably from the existing Triopsidae.

The author included under the family Triopsidae the genera, *Lepidurus*, *Triops* (=*Apus*), *Apudites* Schimper (=*Apus*), and a then new genus, *Prolepidurus*. In other words, priority of the family Apodidae was ignored. This family was erected by Burmeister to include *Lepidurus* "with a flap between the end bristles" and *Apus* "without this flap" (1846, p. 41). Thus, Triopsidae is a synonym of Apodidae.

Protocaris Walcott has been assigned to the order Pseudonotostraca (Raymond, 1935). Tchernyshev's new genera are closest to this genus and unlike those of the Apodidae. Accordingly, the present writer has excluded Tchernyshev's family. Paratriopsidae, from the notostracans and assigned his new genera to the pseudonotostracans.

A further reassignment of Tchernyshev's material is necessary. He established the Triopsidae (=Apodidae) to accommodate a

new genus, *Prolepidurus*. A description of the genus reads as follows (Tchernyshev, 1940, p. 28ff.):

> Carapace elongated and rounded with notch posteriorly. Postocular tubercle high with depression in middle. Similar in the rest to the existing *Lepidurus*. The general structure of their limbs is the same as in the existing *Lepidurus*.

The shape and size of the carapace in living *Lepidurus* species varies considerably (cf. *Lepidurus packardi* and *L. lynchi*. Linder, 1952, pl. 2, figs. 1, 2; pl. 3, figs. 1, 2). In each case there is a posterior notch. Hence, this cannot be significant on the generic level. Secondly, the author states in his description of *Prolepidurus daja* that "the tubercle with a depression in the middle corresponds to the postocular tubercle in *Lepidurus*." It is this tubercle on which the so called nuchal organ occurs. Both its height and location in *Lepidurus* species are fairly uniform (Linder, 1952, p. 28). Therefore, this characteristic can be ruled out as having generic value.

The rest of the generic description acknowledges similarity and sameness to *Lepidurus*. A further point of interest is Tchernyshev's figures of three apparently distinctive telsons bearing supra-anal plates. These represent his three new species of *Prolepidurus: P. daja, P. kuenga*, and *P. schewija*. They are from Transbaikal (L. cret. The presence of a supra-anal plate on the telson is the "main character" of the genus *Lepidurus* (Linder, 1952, p. 30)—and Tchernyshev's figured telsons are typical for this genus.

In light of the above, it seems reasonable to conclude that *Prolepidurus* is an invalid genus and thus it is placed in the synonomy of *Lepidurus*.

RIBEIRIDAE

Schubert and Waagen (1903) discussed the internal structure of *Ribeiria*. They compared a longitudinal section through a living *Apus cancriformis* and an equivalent section through a specimen of the genus *Ribeiria* (1903, figs. 1, 2). They found what they interpreted to be an identity of structural and spatial elements. Recognition of this identity appears to the writer to be largely a subjective matter. Line drawings are figured but are not accompanied by actual photographs. A complicated explanation is provided for obvious differences in structural placement. For example, "*J. innenskelet*" is oriented northwest-southeast in *Apus* while, what is interpreted as the equivalent structure in *Ribeiria*, is oriented northeast-southwest. Again, in the case of the structural element labelled "*U-Schalenumschlag*" it appears perfectly straight in *Apus* but curved in *Ribeiria*. Further illustrations of such discrepancies could be cited.

Kobayashi (1936) referring uncritically to Schubert and Waagen's work, thought that, while "*Apus* may be the nearest animal" to *Ribeiria*, nevertheless, "*Ribeiria* is still quite distinct from *Apus* in the folding of carapace and absence of posterior truncation."

Since nothing is known of the appendages of *Ribeiria* species, one cannot accept the speculation of Schubert and Waagen. Theirs incidentally, is the only important argument put forth for assigning the genus to the notostracans.

Under Arthropoda incertae sedis, a subclass Archeostraca von Stromer, was erected as a catchall for all Paleozoic crustaceans for which only a compressed or depressed carapace was known. Raymond (1935) assigned the following genera to this subclass under incertae sedis: *Euchasma, Eopteria, Ischyrina* Billings, *Technophorus* Miller, *Ribeiria* Sharpe, and *Ribeirella* Schubert and Waagen.

A new notostracan genus *Tolmachovia concentrica* Howell and Kobayashi (1936) was originally assigned to the order Notostraca, family Ribeiridae Kobayashi. This genus was described as resembling *Ischyrina* Billings. The present writer, through the kindness of Professor B. F. Howell, was able to examine a paratype of the new genus. There is no observable morphological similarity between this specimen and the living *Apus* or *Lepidurus*. In fact, its assignment to the Notostraca was based on its similarity to the ribeirids. These, in turn, as observed earlier, were thought to be related to the living *Apus* on the basis of Schubert and Waagen's speculation. Having ruled out that speculation as a valid criterion, I regard *Tolmachovia* as having no place among the notostracans.

In light of the above discussion and assignment of both *Ribeiria* and *Ischyrina* to Archeostraca incertae sedis, *Tolmachovia* is also assigned to this subclass.

PRESENT STATUS OF THE FOSSIL AND LIVING RECORD OF NOTOSTRACANS

Once the confusion in the literature is cleared away, it becomes evident that the sparse fossil record has up to the present shown the existence of only two valid genera of notostracans: *Apus* and *Lepidurus*. This parallels the status of living forms. For example, an attempt was made to split up the genus *Apus* and erect a new genus *Proterothriops* Ghigi, 1921. However, subsequent workers did not consider this a valid genus and it was placed in the synonomy of *Apus* (Barnard, 1929). Thus, at present, the only two living genera recognized are the same as those found in the fossil record.

There is a tendency among neobiologists to lump species of notostracans regardless of worldwide distribution. Thus, Linder (1952, p. 3) found *Lepidurus macrurus*, a species from Asia and Europe, a synonym of the American species *L. couesii*, and South American forms of *Apus*, the same as the North American *Apus longicaudatus*. He also anticipated that "additional species from different continents will be found synonymous." (p. 3)

True fossil notostracans have been reported from the Permian of Oklahoma (a thin sandstone in the Enid formation); the Triassic (Stormberg series of South Africa and the Bunter sandstone); and the Lower Cretaceous of Transbaikal. Each of these have been assigned to new species of *Apus* or *Lepidurus*. In light of the taxonomic practices of neobiologists, it is possible that Ruedemann's (1922) species for example, may be assignable to a living species of *Apus* although a shell gland impression is hardly adequate material for such an attempt. Similarly, Schimper's species *Apus antiquus* may be identical with the living *A. cancriformis*. More fossil material will be needed before the suggestion made here can be pursued further.

It seems to the writer that Permian formations such as the Enid sandstone merit systematic collecting in search of better preserved and more abundant notostracan material. Likewise, geologists working on Mesozoic formations, if alerted to the fact that the shales they encounter may contain impressions of *Apus* and *Lepidurus* species, might begin finding such fossil material. Such finds would be especially valuable to the stratigrapher since a great deal is known of the ecology of notostracans and their fossils could help to approximate more closely the depositional environment in doubtful cases.

ADDENDA

1. A. R. Longhurst (1955, Evolution in the Notostraca: Evolution, vol. 9, pp. 84–86) refers to two additional papers containing information on fossil notostracans. These are by Guthorl and Trusheim. In 1934, Guthorl figured probable notostracan carapaces from Permian beds in the Saar, and in 1938, Trusheim figured European Triassic material. Longhurst believes Trusheim's specimens are identical with *Triops* [=*Apus*] *cancriformis*. He also intimates that *Lepidurus stormbergensis* Barnard (Upper Triassic) is conspecific with living *L. articus*. This view reinforces the present writer's suggestion that Permian and Mesozoic notostracans are probably conspecific with living forms.

2. The use of the family name Triopsidae under which the genus *Triops* Shrank was subsumed (Kükenthal, W., and Krumbach, T., 1926–1927, *Handbuch der Zoologie*, Band 3, Hälfte 1, p. 391), requires some clarification. The family is, as was shown earlier, a synonym of Apodidae. However, the genus *Triops* Shrank [=*Apus*], originally revived by Keilhack in 1909, was probably preferred by the cited authors because, according to the strict Law of Priority, *Apus* should be applied to a genus of birds, *Cypselus* (Gurney, R., 1923, Notes on some British and North African specimens of *Apus cancriformis* Schaeffer. Ann. Mag. Nat. Hist. ser. 9, vol. 11, 496–502; cf. p. 497). However, the basis of this transfer of the name *Apus* "is not, even according to the Rules, by any means secure" (Gurney, 1923, p. 497).

The opinions of three leading students of living notostracans (Gurney, 1923, p. 497; 1924, p. 599; Barnard, 1929, p. 6; Linder, 1952, p. 52, footnote 1) are in concurrence that

both common sense and usage should in this instance have precedence over strict priority.

In light of the above, *Triops* Shrank is rejected in favor of *Apus* Schaeffer.

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MANUSCRIPT RECEIVED DECEMBER 27, 1954

NOTICE ON ZOOLOGICAL NOMENCLATURE

1. Notice is hereby given that the possible use by the International Commission on Zoological Nomenclature of its Plenary Powers is involved in applications relating to the undermentioned names included in Parts 1 and 2 of Volume 11 of the Bulletin of Zoological Nomenclature, both of which parts were scheduled to be published on 31 January 1955:

APPLICATIONS IN PART 1 OF VOLUME 11

Pleurotomaria Sowerby (J.), 1821, validation of (if that name is judged to be invalid), and *anglicus* Sowerby (J.), 1818, as published in the combination *Trochus anglicus*, validation of, and designation of, as the type species of *Pleurotomaria* (Class Gastropoda) (pp. 21–27) (Z. N. [S.] 604).

Pachyceras Bayle, 1878 (Class Cephalopoda, Order Ammonoidea: Jurassic), validation of (pp. 28–32) (Z. N. [S.] 670).

APPLICATIONS IN PART 2 OF VOLUME 11

Rhinopteraspis Jaekel, 1919, validation of (Class Ostracodermi) (pp. 66–67) (Z. N. [S.] 863).

2. Attention is drawn to the proposed suppression of the generic name *Jumala* Friele, 1882 (Class Gastropoda), as a name calculated to give offense on religious grounds. This is the first application made under the Article providing for the rejection of names on the foregoing ground inserted in the Règles by the Paris Congress in 1948. (See 1950, Bull. Zool. Nomencl. 4: 193–194) (pp. 59–65) (Z. N. [S.]307).

Any specialist who may desire to comment on any of the foregoing applications is invited to do so in writing to the Secretary to the International Commission (Address: 28 Park Village East, Regent's Park, London, N. W. 1, England) as soon as possible. Every such comment should be clearly marked with the Commission's File Number as given in the present notice.

(Extracted from a notice dated 25 January 1955, signed Francis Hemming)

RETICULOPHRAGMIUM, N. GEN., A NEW NAME FOR *ALVEOLOPHRAGMIUM* STSCHEDRINA, 1936 (PARS).

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In their important paper entitled "Studies of Arctic Foraminifera" (1953), A. R. Loeblich & H. Tappan briefly discuss the genus *Alveolophragmium* Stschedrina, 1936, which was based on the Recent species *Alveolophragmium orbiculatum* Stschedrina (Stschedrina, 1936).

The new genus *Labrospira* was erected in 1947 by H. Höglund, with *Haplophragmium crassimargo* Norman as genotype (Höglund, 1947, p. 141). *Labrospira* is stated to differ from *Haplophragmoides* in showing an interio-areal aperture instead of an interiomarginal one (ibid., p. 133).

Being convinced that *Alveolophragmium orbiculatum* Stschedrina "is without doubt the same [species] as the common Arctic species *Haplophragmium crassimargo* Norman" (Loeblich & Tappan, 1953, p. 29), the authors concluded that *Labrospira* is a junior synonym of *Alveolophragmium*.

The genus *Alveolophragmium* had been established for *Haplophragmoides*-like forms that reveal an alveolar (labyrinthic) wall structure (Stschedrina, 1936, p. 312; Maync, 1952a, p. 48; 1952b, p. 141; Loeblich & Tappan, 1953, p. 28). According to A. R. Loeblich & H. Tappan, however, the type species, *Haplophragmium crassimargo* Norman, 1892, does not possess such an alveolar wall structure, for the apparent alveoles are "merely the gaps left between the coarse fragments used in constructing the test" (Loeblich & Tappan, 1953, p. 29). This being the case,[1] *Alveolophragmium* does not belong to the labyrinthic group (Spirocyclininae) of the Lituolidae. (It must be stressed that the above conclusions rest on the assumption that *Haplophragmium crassimargo* Norman and *Alveolophragmium orbiculatum* Stschedrina are identical).

Some time ago, the writer deseribed a *Haplophragmoides*-like foraminifer from the Oligo-Miocene of Venezuela which positively possesses a reticulate-alveolar wall structure. Since *Alveolophragmium* was the only representative of *Haplophragmoides* with a reportedly alveolar wall structure, the Venezuelan form was named *Alveolophragmium venezuelanum* (Maync, 1952b). No topotype material of *Alveolophragmium orbiculatum* was, of course, available to the writer, and the only reference was the figures given by Mrs. Z. Stschedrina (1936, text-figs. 1–3). Two other species were also referred by the writer to the genus *Alveolophragmium* because of their labyrinthic wall structure, viz. *A. peruvianum* Maync and *A. reticulatum* (Boomgart).

As *Alveolophragmium orbiculatum* Stschedrina (= *Haplophragmium crassimargo* Norman, fide Loeblich & Tappan) now is reported to disclose a simple arenaceous test, whereas the species of *Alveolophragmium* described by the writer show a true alveolar (labyrinthic) wall structure (Maync, 1952b), the mentioned forms obviously cannot be accommodated in the same genus. Since *Alveolophragmium* is considered to be a valid genus, though it does not exhibit an alveolar wall structure contrary to its etymology, the truly labyrinthic forms of *Haplophragmoides* have to be included in a new genus. In order to emphasize the presence of the diagnostic reticulate-alveolar wall structure as revealed by the type species, *Alveolophragmium venezuelanum* Maync (Maync 1952b, pl. 26, figs. 6–8), the new name *Reticulophragmium* is herewith proposed.

Species of *Reticulophragmium* n. gen.

Reticulophragmium venezuelanum (Maync)
Genotype: *Alveolophragmium venezuelanum* Maync, 1952 [Syn. *Haplophragmoides emaci-*

[1] Thanks to the kindness of Drs. A. R. Loeblich and H. Tappan, the writer was enabled to thin-section and examine some hypotype material of *Alveolophragmium crassimargo* (Norman), derived from Frobisher Bay, Baffin Land (locality 22 in Loeblich & Tappan, 1953, p. 6). This form has definitely a non-labyrinthic wall structure and the detailed description given by the above-mentioned authors has our full support.

atum Renz, 1948 (non Brady, 1884)], Oligocene-Miocene, Venezuela, Trinidad, B.W.I.

Reticulophragmium peruvianum (Maync) (Syn. *Ammobaculites* cf. *A. foliaceus* Cushman & Stone, 1949; *Alveolophragmium peruvianum* Maync, 1952). Paleocene-Eocene, Peru.[2]

Reticulophragmium reticulatum (Boomgart) [Syn. *Haplophragmoides reticulatus* Boomgart, 1949; *Alveolophragmium reticulatum* (Boomgart) Maync, 1952]. Miocene, Java.

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NORMAN, A. M., 1892, Museum Normanianum. Pt. 8, Rhizopoda: Durham.

STSCHEDRINA, Z., 1936, *Alveolophragmium orbiculatum* nov. gen. nov. sp.: Zool. Anzeiger, Leipzig, vol. 114, pp. 312–319 (see Ellis and Messina, 1940, etc., suppl.).

WEISS, L., 1955, Foraminifera from the Paleocene Pale Greda Formation of Peru: Jour. Paleontology, vol. 29, pp. 1–21, pls. 1–6.

[2] A few specimens of *Reticulophragmium peruvianum* (Maync), found in the upper part of the Los Jabillos formation (Upper Eocene to basal Oligocene) on Río Chacaracual, Caicara de Maturín (State of Monagas), eastern Venezuela, were made available to the writer through the courtesy of Dr. J. G. Bursch, Phillips Oil Company, Caracas.

NEW NAME FOR *HIPPONIX FLORIDANUS* PALMER, 1953

KATHERINE V. W. PALMER
Paleontological Research Institution, Ithaca, New York

A. A. Olsson has pointed out that the specific name *Hipponix floridanus* Palmer, 1953 (December) (Palmer, K. V. W., 1953, in Richards, H. G., and Palmer, K. V. W., Eocene mollusks from Citrus and Levy counties, Florida, Part 2, Gastropoda: Florida Geol. Survey, Geol. Bull. No. 35, p. 22) is preoccupied by *Hipponix floridanus* Olsson & Harbison, 1953 (November) (Olsson, A. A., & Harbison, Anne, 1953, Pliocene Mollusca of southern Florida: Acad. Nat. Sci. Philadelphia, Mon. 8, p. 280). The new name *Hipponix levinus* is hereby proposed for *H. floridanus* Palmer.

HERMANITES, NEW NAME FOR *HERMANIA* PURI, 1954*

HARBANS S. PURI
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Doctors Stuart A. Levinson and Giuliano Ruggieri have drawn my attention to the fact that *Hermania* Puri, 1954 (Contribution to the study of the Miocene of the Florida panhandle: Florida Geol. Survey Bull. 36 [1953], p. 267) is preoccupied by *Hermania* Monterosato, 1844 (Nomencl. Conch. medit., p. 147) (Mollusca). I, therefore, propose *Hermanites* Puri, new name for *Hermania* Puri, 1954 (not *Hermania* Monterosato, 1844).

* Publication authorized by the Director, Florida Geological Survey.

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REVIEW

COMPOSITION OF SCIENTIFIC WORDS, by Roland Wilbur Brown. Published and distributed by the author at U. S. National Museum, Washington 25, D.C. 882 pp., cloth, 6×9 inches. $8.00 prepaid.

As one who keeps deploring—innumerable times orally, a few times also in print—the rapid decline in the knowledge of the classical languages among naturalists, this reviewer has some times come to feel like one crying in the wilderness. Thus, he finds the more cause for rejoicing in the work of a man who not only complains about that decline but (to quote the famous word about the weather) does something about it.

The man is Dr. R. W. Brown, a Geologist of the U. S. Geological Survey and Paleobotanist at the U. S. National Museum; the work is the one quoted above. The subtitle calls it, most appropriately, "A manual of methods and a lexicon of materials for the practice of logotechnics."

The main part of this book is a "Cross-Reference Lexicon" of 814 pages. It is preceded by an "Introduction" of 55 pages. After a fascinating exposition of the evolution and the peculiarities of the English language this introduction attempts, under the heading "Nature of Greek and Latin," to familiarize the reader without proper classical training with the essentials of transliteration from, and of the grammar of, those languages. The following section, entitled "Formation of Scientific Terms," contains instructions in logotechnics (or word coining) proper and, thus, constitutes the core of the book. The author's general postulate that scientific "words should be simple, euphonious, pure, and mnemonically attractive, to say nothing of being descriptively appropriate," well deserves to be quoted in full, as does his appeal to biologists in particular that "if a plant or animal is worth describing it surely merits an appropriate, uncriticizable name, and the sacrifice of a little time and energy by the creator in devising such a name. He should find this not only a challenge to his ingenuity, but, in subsequent years, a recurrent pleasure like that brought by all significant, creative work."

Dr. Brown distinguishes three modes of creation of scientific terms: adoption, composition, and arbitrary creation of words. His most explicit instructions deal with the composition of words. They should, for example, encourage name coiners to form a geographic species name by adding the suffixes *arius, anus, inus, aricus* but not *ensis* to the names of localities, provinces, countries, etc., if such names are available in Latin, in a latinized form, or in a language derived from Latin, and end in *us, a, um, ius, ia, ium;* e.g. *romanus, angolana, tridentinus, moravicus.*[1]

As to Latinization, Dr. Brown seems inclined to allow more liberty to authors than this reviewer would. Thus, he (p. 38) leaves it to individual judgment whether to prefer *neomexicana* or *newmexicana*, whereas, in my opinion, only *novomexicana* is permissible. In one issue, which has long been a bone of contention between Latinists and formalists, he sides with the latter, namely, in prescribing formation of genitives indicating commemoration or dedication as follows (p. 548): "Attach *-i* to masculine and neuter proper names ending with any letter except *a*, to which attach *-e*." This is in accord with the letter of Art. 14, paragraph 3, of the Rules of Zoological Nomenclature, it is true, but it leads to barbarisms like *clusiusi* (instead of *clusii* or *clusi*) which sound, to my ear, even more horrible than "*maehrenensis.*"

I do not agree with Dr. Brown's appraisal (p. 34) of the modern usage of uniformly transliterating the Greek diphthongs *ai* and *oi* to a plain *e* as an improvement. As long as *Caenozoic* and *coenobite* were spelled as here rendered, it was obvious to any person with some knowledge of Greek, and readily ascertainable from a Greek dictionary by others, that the first component of the former word is derived from καινός = new, but that of the latter from κοινός = common, whereas the syllables *ceno* in *Cenozoic* and *cenobite* can at first sight be distinguished, as to meaning, neither from each other nor from *ceno* in *cenotaph*, where it is derived from κενός = empty.

[1] Not *maehrenensis*, as Haber (*Fossilium Catalogus. I. Animalia*, pt. 53, 1932, p. 158) proposes to name a Jurassic snail from Moravia (German: *Mähren*).

Nobody familiar with biological nomenclature will be surprised to find that the author deemed the problems of gender, especially the requirement of adjustment of the two terms of a binomial to one another, important enough to devote them a separate section (pp. 50–54).

The Cross-Reference Lexicon aligns not only Greek and Latin synonyms but also those in other languages, both living and dead, with the English key words; thus, it accumulates an immense wealth of information on meaning and etymology of several thousand terms. It furnishes the material to which to apply the directions so well exposed in the Introduction. A bibliography of nearly 130 titles provides a welcome guide to supplementary reading, and a concise Index facilitates the use of the book.

All biologists should assign it a place of preference on their shelves of reference books. The few who do not need it so badly will all the same thoroughly enjoy browsing through it. The many who do need it should carefully consult it every time before proposing a new name. OTTO HAAS

SOCIETY RECORDS AND ACTIVITIES

NOMINATIONS FOR MEMBERSHIP

In accordance with Article 3, Chapter 1 of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society, The list has been approved by the Council of the Society.

APPLEGATE, SHELTON PLEASANTS, Rt. 8, Box 637-A, Richmond, Va.: Joseph K. Roberts, Kenneth E. Caster.

BOYD, WALTER WILLARD, 6701 River Rd., Bethesda, Md.: Joseph K. Roberts, Kenneth E. Caster.

DORMAN, JAMES HUBERT, 1616 Bass Ave., Apt. 3, Columbia, Mo.: Raymond E. Peck, A. G. Unklesbay.

ESTES, RICHARD, Dept. Paleontology, Univ. California, Berkeley, Calif.: R. L. Langenheim, Jr., Joseph H. Peck, Jr., S. P. Welles.

GIFFORD, JOE N., 1707 Otoe St., Lincoln, Neb.: Benjamin H. Burma, Walter Sadlick.

GREEN, ROBERT, 2784 Yale Station, New Haven, Conn.: Joseph T. Gregory, Carl O. Dunbar, Karl M. Waagé.

HENSLEY, FRANK S., JR., 407 South 5th, Laramie, Wyo.: Alan B. Shaw, Mary N. Gilman.

HOUGH, MARGARET JEAN, Room 17, U. S. Nat. Mus., Washington 25, D. C.: Harry S. Ladd, Frank C. Whitmore, Jr., C. F. Gazin.

MCKENNA, MALCOLM C., 241 Las Altos Dr., Berkeley 8, Calif.: R. L. Langenheim, Jr., S. P. Welles, Joseph H. Peck, Jr.

MILLER, HALSEY WILKINSON, JR., Peabody Mus., Yale Univ., New Haven, Conn.: Joseph T. Gregory, Carl O. Dunbar, Karl M. Waagé.

MUELLER, KLAUS J., Dept. Geol., State Univ. Iowa, Iowa City, Iowa: A. K. Miller, W. M. Furnish, Brian F. Glenister.

NAGAPPA, YEDATORE, Digbol, Assam, India: W. Storrs Cole, Margaret Ruth Todd.

PITRAT, CHARLES WILLIAM, 1235 Dartmouth Rd., Madison, Wis.: M. L. Thompson, Walter Youngquist, A. K. Miller.

SAMPLE, JOHN THOMAS, JR.: P.O. Box 1973, El Paso, Texas: Lloyd A. Nelson, W. S. Strain, K. E. Caster.

SANDERSON, GEORGE ALBERT, JR., Shell Development Co., 3737 Bellaire Blvd., Houston 25, Texas: M. L. Thompson, Walter Youngquist, A. K. Miller.

ST. JEAN, JOSEPH, JR., University Apts-3, Bloomington, Ind.: J. J. Galloway, Charles Deiss.

SZMUC, EUGENE JOSEPH, 8370 Wallings Rd., North Royalton, Ohio: Aurèle La Rocque, Mildred Marple.

TRAVERSE, ALFRED, Fuels Microscopy Lab., U. S. Bureau of Mines, Denver Federal Center, Denver, Colo.: F. D. Holland, Jr., Gordon L. Bell, Wilson M. Laird.

ARMSTRONG, AUGUSTUS K., Dept. Geol., Univ. Cincinnati, Cincinnati 21, Ohio. K. E. Caster, Harold K. Brooks.

ARTUSY, RAYMOND L., R.F.D. 166 B, Galveston, Texas, Stuart A. Levinson, Patrick K. Sutherland.

CORTEZ, WILLIAM H., 320 W. Alberta St., Anaheim, California, Myra Keen, Siemon W. Muller.

DE LISE, KNOXIE C., 2773 Foothill Ave., Richmond, California. R. L. Langenheim, Jr., W. O. Addicott, Joseph H. Peck, Jr.

DODGE, HARRY W., JR., Dept. Geol., Univ. Kansas, Lawrence, Kansas. Walter Youngquist, B. F. Howell, M. L. Thompson.

DOUGLAS, WILLIAM B., JR., Box 570, Elko, Nevada. Joseph Lintz, Jr., S. Stewart Williams.

ENBYSK, BETTY J., 2027 E. 135th Pl., Seattle 55, Washington. V. Standish Mallory, Harry E. Wheeler, W. Frank Scott.

HOWE, JOHN A., Dept. Geol., Univ. Nebraska, Lincoln, Nebraska, Benjamin Burma, Walter Sadlick.

JOHNSON, GRACE P., 1545 Stanford Ave., Stanford, California, Mrya Keen, Siemon W. Muller, David L. Jones.

ULMER, JOSEPH W., JR., 6468 Ridge Rd., Cincinnati 13, Ohio. Harold K. Brooks, K. E. Caster, John K. Pope.

NOTICE: As of May 15, 1955 the office of Secretary of the Society will be in charge of Dr. Harry B. Whittington, Museum of Comparative Zoology, Harvard University, Cambridge 38, Mass. Secretary Caster will be working with the South African Geological Survey during the summer of 1955 and beginning September 1 will take up the Work of Visiting Professor at the University of Tasmania, Hobart, Tasmania.